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ARE THERE FOLIAR GAPS IN THE LYCOPSIDA?[1]

EDWARD C. JEFFREY

(WITH PLATES XVII AND XVIII)

Six years ago the present writer published an account of his studies on the stem of the pteridophytes and gymnosperms.[2] In the conclusions not only these large groups were considered, but also the remaining vascular plants, which had been the subject of earlier investigations. The general result was reached "that there are two phylogenetic types of tubular central cylinder, namely, that in which only ramular gaps are present, and that in which both ramular and foliar gaps occur." Further it was stated: "The use of these constant and characteristic anatomical features results in the division of the Vasculares into two great primitive stocks—the Lycopsida, which are cladosiphonic and palingenetically microphyllous, and the Pteropsida, which are phyllosiphonic and palingenetically megaphyllous. The Lycopsida include the Lycopodiales and Equisetales. The Pteropsida include the Filicales, Gymnospermae, and Angiospermae." The opinion was expressed that the Lycopsida and Pteropsida "appear to have been separate back to the beginning of the period when the paleontological record begins." Since the publication of that memoir, the writer has been busily engaged in other directions, and his time has been fully taken up. In the interval a great deal of literature has appeared, especially in European countries, on the anatomy and phylogeny of vascular plants, and not unnaturally the writer's hypothesis has been subjected to the criticism which is the fate of every scientific hypothesis. The most vigorous objections to

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 14.

[2] Phil. Trans. Roy. Soc. London B. 195:119–146. 1902.

the hypothesis, as might be expected, have been raised by those whose published views are prejudicially affected by its validity. In spite of all that has been written on the subject, however, the author has seen no reason to modify his standpoint in any essential feature. It is proposed in the present article to deal with some of the objections, mainly resulting from a misapprehension of the author's statements or an unfamiliarity with the anatomical field, which have been raised against the Lycopsida. In a subsequent article the Pteropsida will receive consideration.

It will perhaps be well at the beginning to define the Lycopsida and Pteropsida in a comprehensive way and to include external characters as well as anatomical ones.

LYCOPSIDA.—Palingenetically microphyllous vascular plants, with ventrisporangiate sporophylls (sporangia adaxial), the tubular central cylinder when present characterized by the entire absence of gaps or interruptions in the fibrovascular tissue immediately above the outgoing leaf-traces.—Lycopodiales, Psilotales, Equisetales, Sphenophyllales.

PTEROPSIDA.—Palingenetically megaphyllous vascular plants, with dorsisporangiate sporophylls (sporangia abaxial), the tubular central cylinder when present characterized by foliar gaps or interruptions in the fibrovascular tissues immediately above the outgoing foliar traces.—Filicales, Gymnospermae, Angiospermae.

It is necessary to define very clearly, on account of numerous misconceptions and misunderstandings, the nature of a foliar gap, for the writer's critics have shown considerable versatility of misunderstanding in regard to this important feature. In one of the more simply organized ferns (Ophioglossum, Osmunda, Schizaea, Mohria, Adiantum, etc.), wherever a leaf passes off from the surface of the stem, it carries with it a fibrovascular strand, the leaf-trace. The foliar trace is derived from the tubular central cylinder of the stem, and as it bends away from the surface of the stele in its outward and upward course, it causes immediately above it, in the stelar wall, an interruption of the fibrovascular tissues, known as the leaf gap. The foliar gap may be distinguished from other gaps in the wall of the fibrovascular hollow cylinder by the fact that it occurs immediately above a leaf-trace. A true foliar gap, moreover, is always

related to but a single leaf-trace. If several traces appear in relation to a stelar gap, and especially if they are related to the *sides* of the gap, it may be concluded at once that no true foliar gap is present. It may be added for the benefit of inexperienced anatomists that not all gaps in the wall of the central cylinder are foliar gaps. Where the fibrovascular tissues are much reduced in amount, as is not unfrequently the case, they often break up into a loose meshwork, which has no necessary relation to the vascular supply of the leaves or the branches.

Lepidodendreae and Sigillariae

In the memoir cited above, the writer has called attention to the fact that in the Lepidodendreae, which are among the oldest of the Lycopsida, there are no foliar gaps in the tubular central cylinder, when present. *Fig. 9* illustrates this feature in *Lepidophloios Harcourti*. Below in the figure is to be seen the woody cylinder, showing inferiorly some of the thin-walled tissue of the pith. The cylinder is dentate on its outer surface, and the teeth are composed to some extent of small-celled protoxylem. Outside the wood may be seen nests of small cells, which mainly lie in the intervals between the dentations. These are the foliar traces. It is clear that there are no gaps or interruptions in the central cylinder corresponding to these. Consequently it may be stated that there are no foliar gaps in the species figured. An examination of a considerable number of sections of lepidodendrid stems has made it clear that foliar gaps are absent in the group.

In the older Sigillariae the primary wood in the stem ordinarily formed a continuous cylinder, and there were, as in Lepidodendron, no gaps of any kind except for the outgoing strands of branches. In more modern Sigillarias, however, the woody cylinder was frequently entirely or partially broken up into separate strands. *Sigillaria elegans* from the Lower Coal Measures had the continuous type of woody cylinder, while *S. Menardi* from the Permian had separate strands of wood constituting its tubular stele.[3] The leaf-traces in both types of Sigillaria stem, however, passed off without leaving any foliar gaps in the central cylinder, for in the Sigillarias of the more

[3] Kidston, R. Internal structure of *Sigillaria elegans*. Trans. Roy. Soc. Edinburgh **41**:533–550. 1905.

modern type, with the cylinder broken up into numerous bundles, the gaps between the strands were not subtended by the leaf-traces, which took their origin from the face of the fibrovascular bundles. This fact it is very important to keep in mind, in view of the conditions to be found in some of the reduced Lycopsida to be described later. It is further of interest to note that these arboreous lycopods, in which the leaves were sometimes a meter in length, offer no exception in their anatomical structure to the writer's definition of the Lycopsida.

LYCOPODIACEAE

Under this heading Lycopodium itself need not be considered, as it has a solid protostelic central cylinder. Phylloglossum, however, has a tubular stele, which in the lower tuberous portion of the stem constitutes in cross-section an almost continuous horseshoe of xylem, without foliar gaps for the relatively large radical leaves (protophylls). The opening in the horseshoe corresponds to the outgoing strand which passes into the resting tuber, forming the next year's plant. Above the tuber the stem of Phylloglossum passes into the slender peduncle of the cone. In this region of the stem the fibrovascular tissues separate into a number of distinct strands, comparable to those found in the axis of the less ancient Sigillarias. *Fig. 8* is a copy of a figure by BERTRAND,[4] showing the manner in which these isolated peduncular strands give rise to the traces of the lower sporophylls of the cone. It will be noted on the lower side of the figure that the bundles are much elongated radially. In such cases they are about to give off sporophyll traces. In the upper part of the figure three outgoing traces are seen, in different degrees of detachment from their corresponding peduncular strands. On the left, one of the traces has turned obliquely after leaving the peduncular strand, so that it nearly subtends the hiatus between two peduncular strands. An inattentive observer might readily interpret the hiatus as a real foliar gap. Only a consideration of the mode of origin of the trace from the peduncular strand makes the real condition of affairs apparent. There are clearly no foliar gaps present, else the peduncular strands would fork above the outgoing traces. The conditions in the upper part of the stem of Phylloglossum are clearly similar to those obtain-

[4] Phylloglossum. Archives Bot. du Nord de la France **1885**:112. *fig. 102.*

ing in a Sigillaria with separate fibrovascular strands. In the cone of Phylloglossum individual sections often present an appearance still more misleading. In *fig. 10* is shown such a condition. A horse-shoe-shaped fibrovascular mass appears in the center, and opposite its opening a sporophyll trace. To the right and left below are two other foliar traces. An inexperienced anatomist might readily conclude that the gap opposite the uppermost trace was a true foliar gap. *Fig. 11* shows a section from another cone, with two such apparent foliar gaps, one on each side, each apparently subtended by its corresponding leaf-trace. *Fig. 12* shows another section from the same cone, a small fraction of a millimeter lower down. It is here to be noted that the foliar trace on the right in the preceding figure joins the *face* of the large cauline fibrovascular strand, forming the same radially elongated mass as is characteristic of the outgoing sporophyll traces shown in *fig. 8* from the peduncle. Still lower down, as was learned from the study of serial sections, the foliar strand on the left joined the outside of its cauline strand in a similar manner. A study of the cone of Phylloglossum has shown that the traces for the sporophylls invariably pass off from the outer surface of the central cylinder without leaving any real foliar gaps. Sometimes two or even three traces may originate along the margins of the same hiatus in the stele. The interruptions in the central cylinder or stele are no more to be regarded as foliar gaps than are the corresponding ones in certain Sigillarias. It is obviously impossible with any clear eye to anatomical relations to regard the perforations which exist in the upper part of the fibrovascular system of the stem in Phylloglossum as being of the nature of foliar gaps. Miss SYKES has recently reached the conclusion that the living Lycopodiaceae originated in all probability by reduction from the more complex arboreous lycopods of the Paleozoic period.[5] Without presuming to indorse this view, it may be pointed out that it stands in the way of presumably reduced modern lycopodineous forms in any case possessing the foliar gaps which were denied to their supposed Paleozoic ancestors, which possessed very much larger leaves.

[5] Morphology of the sporangium-bearing organs in the Lycopodiaceae. New Phytologist 7:41–60. 1908.

PSILOTACEAE

Fig. 6 shows a magnified view of the stem of *Tmesipteris tannensis*, as viewed in transverse section. On the lower left side is a blunt projection from the surface of the stem, the base of a sporophyll.[6] At the top of the figure is another sharper projection, which is the basal portion of a foliage leaf. Subtending each of the projections from the surface of the stem noted above is a fibrovascular strand, which has recently come off from the central cylinder. *Fig. 7* shows part of the foregoing more highly magnified, to make clear the relations of the outgoing traces to the stele of the stem. With the greater magnification an additional trace can be seen emerging from the central cylinder on the lower right hand. In passing out none of these three traces subtends a gap in the central cylinder, which in this region is a continuous fibrovascular tube. In the upper region of the stem, particularly where it gives rise to sporophylls, as BERTRAND has pointed out,[7] the central cylinder breaks up into separate strands, much as happens in the upper part of the axis of Phylloglossum. In isolated transverse sections one often sees appearances such as are represented in *figs. 10* and *11* of the present article. On the strength of such evidence Miss SYKES[8] has asserted that there are foliar gaps in Tmesipteris. Her own figures, however, cannot be reconciled with this statement. On page 71 she represents sections taken at various heights through a portion of the stem, and makes a diagram of the bundle arrangement in this region. According to her figures the gaps are mainly on one side of the central cylinder or stele, and no less than three traces are related to one of these, that is, they are derived from the fibrovascular strands along its *lateral* margins. Three other traces originate near smaller stelar lacunae and one comes off remote from any gap. A greater inconstancy in the mode of origin of traces could scarcely be imagined. A general acquaintance with fibrovascular anatomy should make it clear that true foliar gaps in the same region of the stem should be nearly of a size and should occur immediately *above a single* leaf-trace. This state of affairs is

[6] Miss SYKES prefers to regard this as a *fertile branch*.

[7] Recherches sur les Tmesipteridées. Archiv. Bot. du Nord de la France **30**:—. 1882.

[8] Anatomy and morphology of Tmesipteris. Annals of Botany **22**:63–89. 1908.

very far from being realized in Tmesipteris as described by Miss SYKES. The conditions are in fact the same as those found in the corresponding region of the stem in Phylloglossum. Miss SYKES has been so good as to loan her sections, and the series, although not complete, vouch for the general accuracy of her figures. One fact of importance appears, however, to have escaped her notice, although it is clearly indicated in the sections, namely, that in every case the outgoing strands of appendages originated *opposite* the strands of the central cylinder and did not subtend any gap *at their point of origin*, although some of them by a subsequent oblique course, as in Phylloglossum, seemed to subtend the stelar gaps. Appearances of this kind have been brought to the attention of Professor BOWER, and he figures one such section on page 420 and again on page 487 of his recent work.[9] He expresses the opinion that his figure overthrows the hypothesis of JEFFREY on the lycopsid side. He further adds in a footnote: "The Botryopterideae are not phyllosiphonic; thus the anatomical distinction of JEFFREY breaks down on both sides." In this added statement he is even less happy than in the original one, for he is apparently unaware that ferns with a protostelic central cylinder cannot possibly be phyllosiphonic, that is, possess foliar gaps. In all of the Botryopterideae in which the origin of the foliar strands has yet been described the central cylinder is protostelic. Professor BOWER is in general not entirely at home in discussing anatomical facts. As a further example of this, may be cited his statement that *Alsophila excelsa*, as described by GWYNNE-VAUGHAN, shows a "transition from the cladosiphonic to the phyllosiphonic" condition in the young plant. Professor TANSLEY in a review of Professor BOWER'S book[10] very properly criticizes this singular misunderstanding in the following words: "Mr. GWYNNE-VAUGHAN will be probably surprised to learn that he has shown a 'transition from the cladosiphonic to the phyllosiphonic' state in *Alsophila excelsa*. What really exists, of course, is a transition from protostely to siphonostely, and protostely is not a monopoly of the microphyllous forms, but is found equally among the primitive ferns." It cannot be too strongly emphasized that, especially in difficult cases,

[9] The origin of a land flora. London. 1908.

[10] New Phytologist **7**: 126. 1908.

like those occurring in the reduced Lycopsida, thin serial sections are necessary to a proper understanding of the real anatomical relations. It may be stated in conclusion that there are no real foliar gaps in Tmesipteris and that statements as to their presence depend on errors of observation and interpretation.

In Psilotum leaf-traces are absent in the case of the vegetative leaves, but as the angles of the stellate central cylinder subtend the ridges of the stem from which the leaves take their origin, there can be no question of the presence of foliar lacunae in this genus. Traces are present in the case of the sporophylls, but as these in general occur on the smaller terminal branches, where the stele is solid, they do not serve to elucidate the subject. It is of particular interest that the leaf-traces should sometimes disappear altogether in the case of the small-leaved forms (the Lycopsida). The writer has called attention to this condition as occurring in the case of the basal foliar sheaths of the smaller branches of Equisetum.[11]

EQUISETALES

It is in regard to the supposed existence of foliar gaps in the equisetal series that the writer has received the most weighty criticism. Dr. SCOTT in his masterly treatment of Paleozoic botany in *Progressus rei botanicae*, adopting the present author's division of vascular plants into two phyla, the Lycopsida and Pteropsida, states that it is "open to much criticism; the general grouping however has sufficient claims to be a natural one, to afford at any rate a basis for the discussion of affinities." The only feature "open to criticism" upon which Dr. SCOTT lifts the veil is in regard to the absence of foliar gaps in Equisetum. His words are as follows: "The absence of foliar gaps, upon which JEFFREY lays stress, may hold good in the case of Archeocalamites, but if I rightly interpret the structure, they are present in the Calamariaceae as well as in the recent genus." It will be the writer's task to show that not only are foliar gaps absent in the older genera of the Equisetales, but that they also do not occur in the living genus Equisetum.

Professor CAMPBELL'S criticism of the present writer's work on

[11] Structure, development, and affinities of Equisetum. Boston Soc. Nat. Hist. Memoirs 5: no. 5. p. 176.

Equisetum[12] carries less weight on account of his lack of first-hand familiarity with the extinct members of the Equisetales, a necessary basis for the discussion of a group which has its history so largely in the past. His first objection is that the vascular system of Equisetum is, on the basis of growing point development, of cortical origin and consequently cannot belong to the central cylinder, a term which in this case, according to Professor CAMPBELL, must be restricted to the pith, since it alone takes its origin from the sacrosanct region of the plerome. It is perhaps too late to discuss conclusions drawn from growing point morphology; they often lead rather to a *reductio ad absurdum* than to any useful or logical results. Professor BOWER has set a very good example in his recent book in throwing the growing point theory and the octant theory overboard.[13] Professor CAMPBELL sees no reason why there should be an attempt to reduce the vascular system of Equisetales to either of the types found in the other phyla of the pteridophytes. He further adds that the equisetal series presents resemblances which "indicate a real although extremely remote relationship with the lower ferns," thus committing the very error he previously condemned. Professor CAMPBELL also attaches a good deal of importance to the presence of multiciliate antherozoids as an indication of affinities, and regards this feature both in the Equisetales and Isoetaceae as indicative of filicinean affinities. His views in both instances are at variance with those of modern paleobotanists.

It will be well in our discussion of the Equisetales to begin with the living genus and thence go backward, for only in the living form is it possible to study the anatomical relations with necessary completeness. The reproductive axis of Equisetum will also afford a better starting-point than the vegetative, since it is a well-established principle of the new morphology that the reproductive structures are more likely to retain ancestral characters than the vegetative ones. *Fig. 3* shows a longitudinal section through one of the fibrovascular strands of the cone of *Equisetum telemateia*, at a region where a trace is being given off to a sporophyll. It will be noticed that the sporophyll trace passing off on the left of the figure goes outward and

[12] Affinities of the genus Equisetum. Amer. Nat. 39:273–285. 1905.

[13] Origin of a land flora, chaps. 14 and 42.

upward, without causing any break in the continuity of the fibro-vascular strand of the axis from which it is derived. On the inner side of the axial strand is to be seen a longitudinal space, the protoxylem lacuna. This is continuous through the nodal region in the cone, although in the vegetative axis, as will appear below, the lacuna is interrupted below each so-called zone of nodal wood. The condition of continuity through the nodal region presented by the protoxylem lacuna in the cone of Equisetum is paralleled by similar conditions described by WILLIAMSON in the nodal region of Calamites. *Fig. 2* represents a transverse section through the cone of the same species of Equisetum which makes clear the topography of the sporophyll trace and its corresponding axial strand as seen in this plane. There is no indication of any gap in the strand of the axis corresponding to the outgoing leaf-trace, which exactly subtends it. The examination of a large number of sections has convinced the author that foliar gaps do not in any case occur in the cone axis of Equisetum in connection with the passing-off of the traces of the sporophylls. The sporophyll trace is only about one-third to one-fourth the magnitude of the axial strand from which it arises, and consequently if any indication of a gap were present it would be clearly recognizable. *Fig. 1* shows a general view of a cross-section of the cone of *Equisetum telemateia*, indicating the relation of several sporophyll traces to their corresponding axial bundles. In the cone the foliar traces are vertically somewhat displaced on account of the crowded arrangement of the peltate sporophylls, so that even in accurately transverse sections all of them are not cut at the same level. On the left of the figure a trace has recently left its corresponding axial strand. The next foliar trace to the right is much farther out in the cortex than the first. The interval, corresponding to the next axial strand, does not show a trace, as this is not in the plane of section for the reason indicated above. In the case of the fourth trace the conditions are much as they are in the second; while the fifth trace is just leaving its axial strand. It will be seen by inspection of the whole figure that in each case where a sporophyll trace is present, it subtends the axial bundle from which it was derived in the lower part of its course. There is accordingly no foliar gap present. These micro-anatomical results only serve to confirm the

statement made by the author, in his memoir on Equisetum, concerning the frequent failure to alternate at the nodes, which is characteristic of the strobilar strands of that genus. This feature is illustrated photographically in *pl. 30, fig. 3*, of the memoir. The author's critics do not appear to have found this evidence sufficient. It is important to insist on the correspondence of the micro-anatomical absence of leaf gaps in the cone of Equisetum with the non-alternation of the axial strands of the cone at the nodes, because in some of the fossil forms we have only the latter evidence to go upon. It is perhaps a wise conservatism on the part of Dr. SCOTT to reject the evidence based on the frequent lack of alternation at the nodes, as seen in preparations of the bundle course in the cone of Equisetum. He can scarcely fail to be convinced by the microscopic demonstration of the absence of foliar gaps which has been given above and as represented in *figs. 1, 2*, and *3*. If it is reasonable to define a foliar gap as a gap in the wall of the stele, or one of its component strands in case the stele is not a continuous hollow cylinder, immediately above a leaf-trace, there are certainly no foliar gaps in the cone of Equisetum. The writer has satisfied himself that foliar gaps do not occur even when there is more or less complete alternation of the strands in the cone. *E. telemateia* has been chosen for illustration on account of the large size of the structures present. Similar results in every way are shown by *E. arvense* and *E. hiemale*.

It is now possible to turn with advantage to the examination of the outgoing foliar traces of the vegetative branches of Equisetum. As is well known, the internodal bundles of one segment of the stem in Equisetum alternate with those of the next, in this respect presenting a contrast to the condition of the strands in the cone and in the more ancient extinct genera of the phylum. The internodal strands of successive segments of the stem are joined in the region of the nodes by the so-called "nodal wood," which consists of a dense mass of short reticulated tracheids forming a completely closed ring. *Fig. 5* shows a longitudinal section through an outgoing leaf-trace and its corresponding cauline bundle. A large lacuna, the protoxylem cavity, is seen on the right of the axial strand. This disappears below the so-called "nodal wood." The outward course of the foliar trace is steeply upward, in contrast to that of the sporophyll

trace. Its tracheids obviously take their origin in the region of the protoxylem lacuna and below the "nodal wood." If the usual definition of a node be accepted, as marked by the outgoing leaf-traces, the so-called "nodal wood" of Equisetum in reality is above the node. *Fig. 4* shows a transverse section through a part of the "nodal wood" intervening between the bases of two branches. The leaf-trace lies just outside the mass of reticulated tracheids which compose the wood of the "node." It is obvious that there is no break in the mass of tracheids corresponding to the leaf-trace. Above the incorrectly designated "nodal wood" are the internodal bundles of the next segment of the stem, and between these are parenchymatous gaps, which on account of the alternation of the internodal bundles in different segments are above the leaf-traces, since the latter take their origin from the bundles of the lower internode. Professor CAMPBELL and Dr. SCOTT regard these as foliar gaps. They lack, however, one important feature of foliar gaps, for they do not occur *immediately above the traces*, as should be the case with true foliar gaps. All other foliar gaps with which we are acquainted show this feature. The *onus* of proving that the internodal lacunae of Equisetum are really foliar gaps appears consequently to lie upon the investigators who claim that they are to be regarded as such. It will be clear from the anatomical facts described above that in view of the relation of the leaf-traces to the so-called "nodal wood" it is quite incorrect to designate the ring of tracheids which lies *above* the outgoing leaf-traces as "nodal wood." It can only be called accurately supranodal wood. This distinction is a very important one to make, moreover, on phylogenetic grounds.

As a sequel to the description of the actual anatomical relations of the outgoing leaf-traces of the vegetative stem of Equisetum, it is natural to proceed to the discussion of the evolutionary or phylogenetic significance of the observed facts. The following citation from the memoir on Equisetum may appropriately be introduced at this point: "But STUR has shown that in the Ostrau beds, passing from the lower to the higher strata, a series of forms, *Calamites ramifer* Stur, *C. cistiformis* Stur, *C. approximatiformis* Stur, and *C. ostraviensis* Stur, represents transitions from the bundle arrangement of Archeocalamites, represented in *pl. 1, fig. 15*, to that of Equi-

setum, represented in *pl. 1, fig. 16.*" It is obvious from the data of STUR, which have never been called in question, that the older Calamites were without the alternation of the strands in the region of the nodes which is characteristic of the more modern Calamites and the stem of the living Equisetum. It will be clear from the description of the anatomical conditions present in the cone of Equisetum that absence of alternation brings with it the complete absence of foliar gaps. The writer in his memoir has suggested that the explanation of the peculiar features of the foliar traces in the vegetative stem of Equisetum is to be found in the past history of the phylum to which it belongs. Dr. SCOTT would probably agree to the soundness of this proposition, for example, in the case of the older living gymnosperms. There appears to be no reason to make an exception in a group which has at least so long a past as the Gymnospermae. In the non-alternating arrangement of the internodal strands, characteristic of the stems of the older Calamites (which is still largely represented in the cone axis of the living genus), there were no foliar gaps immediately above the outgoing foliar traces. As the relations of the internodal strands of one internode to those of the next became changed in the progression from the archeocalamital to the equisetal mode of arrangement, the leaf-traces naturally came to lie opposite the gaps between the internodal strands of the next higher segment of the stem. But with the conservatism which is one of the most interesting characters of leaf-traces in general, they retained in Equisetum their old anatomical relations to the central cylinder of the stem. That is, they still pass off in the vegetative stem of Equisetum without leaving any true foliar gaps. The lacunae in the internodes cannot be regarded as foliar gaps, since they are not *immediately* above the foliar traces, but are separated from them by the depth of the so-called "nodal" wood! The explanation offered is a reasonable one in view of the past history of the group, and on those who do not accept it is placed the burden of some other more reasonable elucidation of the peculiar anatomical relations of the leaf-traces in the genus Equisetum.

The writer is credibly informed that Dr. SCOTT is of the opinion that the internodal gaps in the genus under discussion are *de facto* foliar gaps. This is a somewhat surprising opinion on the part of

one whose brilliant investigations on the anatomy of the cycadean peduncle have put the whole subject of the affinities of the cycads with the lower extinct gymnosperms in a new light. Dr. SCOTT from his discovery of centripetal xylem in the peduncles of the reproductive axes of certain living cycads reached the conclusion that their ancestors with strong probability possessed similar bundles in their vegetative stem. This condition is in fact realized in certain of the Pteridospermeae, particularly in Lyginodendron, which Dr. SCOTT regards as a probable ancestor of the cycads. There can be no question that Archeocalamites and Calamites are very much more nearly related to Equisetum than is Lygindodendron or any similar form to the living cycads. It follows that the reproductive axis of Equisetum is much more likely to perpetuate the ancestral characters of its stock than is the cycadean cone. It appears to have been shown above beyond any doubt that the equisetaceous strobilus perpetuates both the non-alternating strands and the complete absence of foliar gaps of the oldest calamitean forms. In the light of these facts there can be no reasonable doubt that the peculiar anatomical relations of the vegetative foliar traces of Equisetum are likewise persistently retained indications of the ancestral condition, for although the shifting of the internodal strands in the course of evolution has caused them to subtend the gaps between the strands of the next upper internodes, they still leave the central cylinder without giving rise to true foliar lacunae, and are moreover separated from their apparent gaps by the whole depth of the supranodal wood. Collateral evidence of the correctness of this view of an even more cogent kind has been discovered, but is reserved for a subsequent communication.

The older members of the equisetal alliance may now be considered. WEISS in one of his superb and classic monographs on the Carboniferous Calamites[14] has published a number of illustrations of calamitean cones. On *pls. 1* and *2* are figures of the genus Stachannularia, which show clearly the phenomenon of non-alternation at the nodes of the cone. *Pls. 3* and *4* show the same phenomenon in the well-known genus Calamostachys. In *pl. 9* a similar condi-

[14] Steinhohlen-Calimarien. Atlas zu denAbhandlungen Gelog. Specialkarte V. Preussen 2[1]: Berlin. 1871.

tion is figured in the cones of the remarkable genus Cingularia. Our information on the subject of the strobilus of the important calamitean genus Palaeostachya has recently been materially increased by the important investigations of HICKLING.[15] This author states: "From an examination of the numerous sections cut more or less transversely through the node, I feel little doubt that no regular pectination occurred; while on the other hand one or two sections showed features which seemed explicable only on the assumption that an occasional communication (probably irregular) did occur between adjacent bundles." The conditions in this genus of calamitean cone would seem accordingly to have approximated very closely those existing in the strobilus of the modern Equisetum, so far as the course of the bundles in relation to the nodes was concerned. This resemblance is all the more striking because, lower down on the same page, the author states that the sporophyll trace left the axial strand without giving rise to any foliar gap. His words are "*no gap is left in the main bundle.*" The italics are those of the present writer. "The main bundle" here means the bundle of the axis from which the sporophyll trace was derived. It will be readily inferred from the various citations given above that, in spite of the conviction expressed by Dr. SCOTT that foliar gaps occurred in the vegetative stem of the Calamites, they must have been generally absent in the cones of the more important calamitean types. There seems accordingly little reason to doubt, when the foliar relations of the more modern Calamites are fully worked out, since the course of their internodal strands resembled that found in Equisetum, that they will prove to be very similar to those of the living genus; and, in view of the similarity shown above in the fibrovascular arrangements of the cone, will be susceptible of a similar interpretation. This follows all the more certainly because so distinguished an authority as Dr. SCOTT himself states, in his *Studies in fossil botany:* "Thus the calamite, so far as anatomy goes, is simply an Equisetum with secondary thickening."

The conditions in Archeocalamites, the oldest calamitean genus, are particularly significant. In this form one of the most characteristic features was the failure of the primary fibrovascular strands of the vegetative stem to alternate at the nodes, as they do in the more

[15] Anatomy of *Palaeostachya vera.* Annals of Botany **21**:375. 1908.

modern Calamites and in Equisetum. It follows that there could have been no foliar gaps in this genus, if the general anatomical conditions were like those found in the rest of the calamitean stock, as has already been indicated by the present writer in the memoir on Equisetum. Our knowledge of the cone of Archeocalamites is very incomplete and nothing is known of its anatomical structure.

It may be stated with some confidence, if credence is to be attached to the doctrine of descent and to the general principles of modern plant anatomy, that the equisetal stock entirely lacks foliar gaps immediately above the outgoing leaf-traces. Dr. SCOTT's statement that in respect to their vascular anatomy the Equisetales "reach the level of the simpler gymnosperms or dicotyledons" (*Progressus rei botanicae*, p. 157) will apparently, as a consequence, need some revision. There further seems to be no reason to doubt that the Equisetales are quite typical Lycopsida in the sense defined in the writer's two memoirs, and are as a consequence far removed from any mere affinity with any of the pteropsid series.

It may be added that there seems to be no reason at the present time, on anatomical grounds at any rate, to suppose that the Pteropsida had a sphenophylloid or ophioglossaceous origin from the Lycopsida. Neither Pseudobornia, of the reproductive organs of which we know little and of the anatomical structure of which we are entirely ignorant, nor Ophioglossum, of which the characters anatomical and reproductive are entirely filicinean, can serve as a phylogenetic link between the primitively small-leaved ventrisporangiate (adaxial) forms (Lycopsida) and the palingenetically large-leaved dorsisporangiate (abaxial) forms (Pteropsida). As Professor TANSLEY has recently put it in a review of Professor BOWER's *Origin of a land flora*,[16] "on the general point of the relation of the 'microphyll' to the 'megaphyll,' there is no evidence of any capacity of the microphyll to evolve the megaphyll."

Summary

1. True foliar gaps occur *immediately above* their corresponding leaf-traces and are not *lateral* to the leaf-traces.

2. Foliar gaps are absent in Phylloglossum, although a super-

[16] New Phytologist 7:125. 1908.

ficial examination of the anatomy of this genus might lead to the conclusion that the perforations in the tubular stele, which are sometimes *lateral* to the outgoing leaf-traces, are to be regarded as true foliar lacunae.

3. Foliar gaps are likewise absent in Tmesipteris, and recent statements as to their presence are based on misinterpretation or misconception. Perforations in the stele are here also found sometimes *lateral* to one or *more* leaf-traces, but these cannot be regarded as true foliar gaps.

4. Foliar gaps are absent in the Lepidodendreae and the Sigillariae, but in the more modern species of the latter perforations of the tubular central cylinder are sometimes found, which have the same relations and are susceptible of the same explanation as are the similar perforations in Phylloglossum and Tmesipteris.

5. Foliar gaps are unquestionably absent in the cone axis of Equisetum, and on the basis of comparative anatomy are absent also in the vegetative stem. Similar statements apply to the reproductive and vegetative axes of Calamites. Archeocalamites has no foliar gaps in its vegetative stem.

6. The Lycopsida as defined by the author are clearly marked off from other plants by a palingenetically microphyllous habit, the absence of foliar gaps in the tubular stele, and by the possession of sporophylls with adaxial sporangia. They constitute a great natural phylum.

In conclusion the writer wishes to express his thanks to Miss Sykes, Professor A. A. Lawson, Professor G. J. Pierce, Dr. Holman (Stanford University), and Mr. L. A. Boodle for material which they have kindly put at his disposal.

Harvard University

EXPLANATION OF PLATES

PLATE XVII

Fig. 1.—Transverse section of part of the cone of *Equisetum telemateia*. ×15.

Fig. 2.—Transverse section showing the axial bundle and its outgoing foliar trace of the cone of *E. telemateia*. ×25.

Fig. 3.—Longitudinal section of the same. ×25.

Fig. 4.—Transverse section through the supranodal wood of the vegetative

axis of the same species of Equisetum, showing the absence of a foliar gap corresponding to the leaf-trace which lies in the cortex. ×25.

FIG. 5.—Longitudinal section through a vegetative node of the same species of Equisetum, showing the departure of the leaf-trace without causing any gap in the supranodal wood. ×25.

PLATE XVIII

FIG. 6.—Transverse section of the stem of *Tmesipteris tannensis*. ×15.

FIG. 7.—Tranverse section of the same, showing the relation of the outgoing traces to the central cylinder. ×30.

FIG. 8.—Copy of a figure from BERTRAND, showing the departure of the traces of the lower sporophylls from the upper region of the peduncular strands in Phylloglossum.

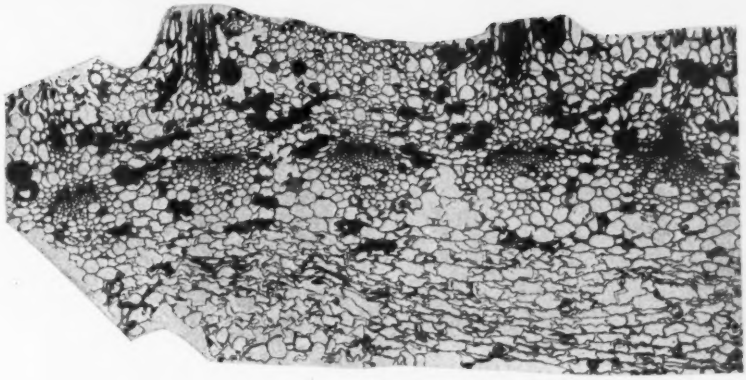
FIG. 9.—Transverse section of part of the central cylinder of *Lepidophloios Harcourti*.

FIG. 10.—Transverse section through the middle region of the cone in Phylloglossum, showing the relation of the leaf traces to the central cylinder. ×60.

FIG. 11.—Transverse section through the central region of the cone in another example of Phylloglossum, showing two apparent "foliar gaps." ×60.

FIG. 12.—Transverse section through the same cone slightly lower down, showing the connection of the foliar strand with the side of the apparent foliar gap. ×60.

NOTE.—*Figs. 10, 11, 12* are all made from herbarium specimens. In *fig. 12* the action of caustic alkali has not quite restored the size of the cells in the gap on the right of the central cylinder; it should appear the same size as that shown on the right of *fig. 11*.



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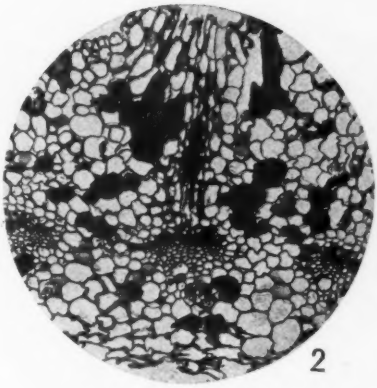

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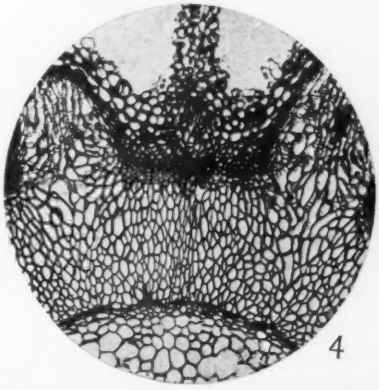

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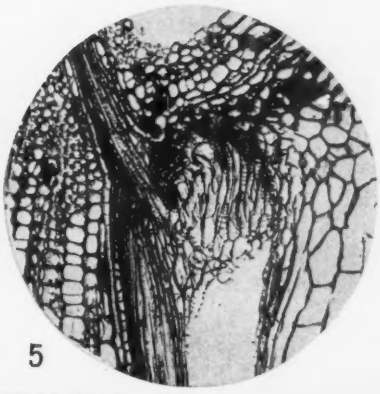

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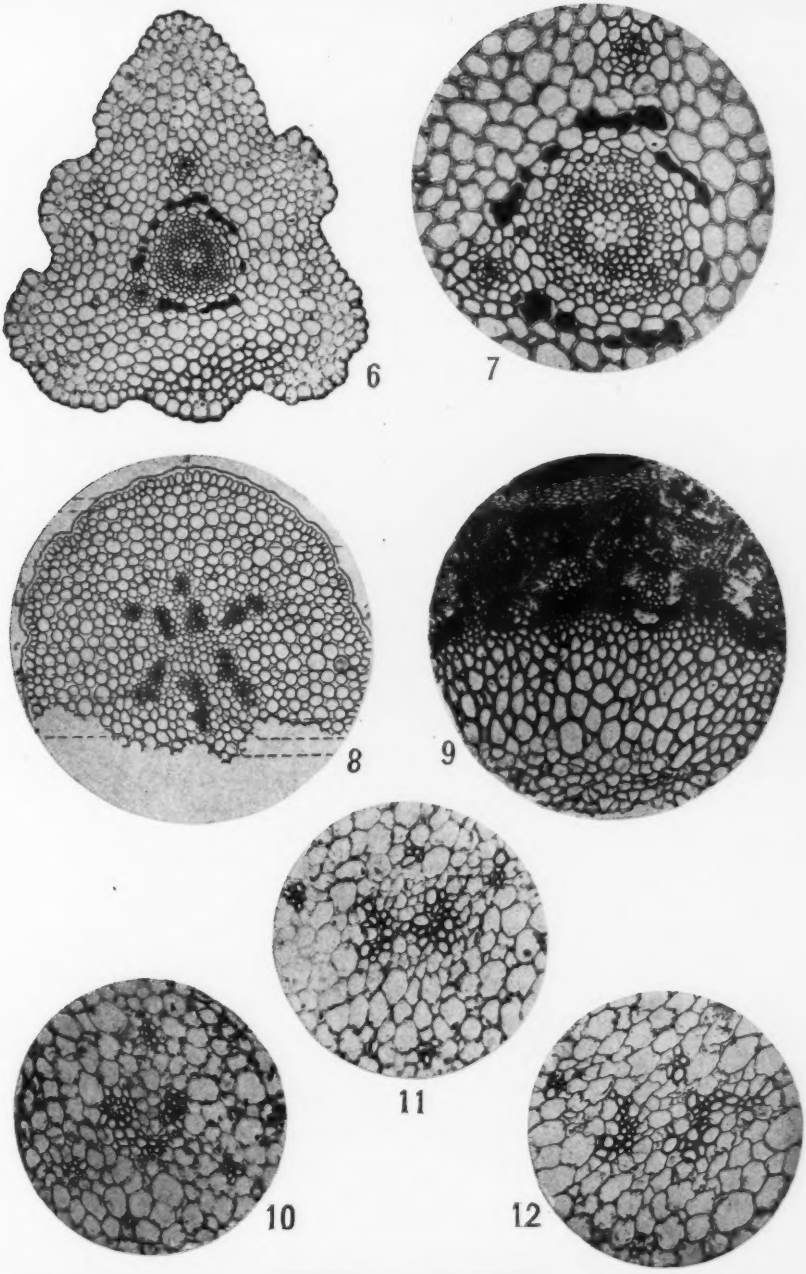
JEFFREY on LYCOPSIDA



JEFFREY on LYCOPSIDA

EFFECT OF ILLUMINATING GAS AND ETHYLENE UPON FLOWERING CARNATIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 116

WILLIAM CROCKER AND LEE I. KNIGHT

(WITH FOUR FIGURES)

1. Historical

As early as 1864 observations were recorded on the effect of illuminating gas on vegetation. GIRARDIN (1) called attention to the phenomena of gas injury to trees as reported from various places in Rouen, Berlin, Hamburg, Hanover, etc. He especially investigated injury done to Italian poplars which had come into use as shade trees along the highways. He made a chemical analysis of samples of soil taken three feet from leaks in the gas pipes, and found inflammable oil as well as sulfur and ammonia compounds present. R. VIRCHOW (2) expressed an opinion that coal gas is especially injurious to vegetation. KNY (3) was one of the first to test the injury experimentally. He used three sound trees in the Berlin Botanical Garden, each about twenty years old—one maple and two lindens. Gas pipes were carefully laid 84^{cm} deep and the gas used was freed of sulfuretted hydrogen. The two pipes were laid in a circle about the maple, and four burners were attached at a distance of 118^{cm} from the trunk. Near each linden tree were two burners, 110^{cm} from the trunks. The gas escape was measured daily.

(1) Maple received daily..... 12.9 cubic meters
(2) First linden..... 11.7 cubic meters
(3) Second linden..... 1.6 cubic meters

The experiment was begun July 7 and lasted for (1) and (2) a half-year, for (3) a full year. First a Euonymus (*E. europea*) near the maple died, then the maple lost its leaves (September 1). At the same time an elm near by showed injury. September 30 the first linden showed signs of injury. On October 12 the first linden lost its leaves, and on October 19 the second, while other lindens in the garden were yet green. An examination of roots one-half inch in diameter showed a blue coloration extending out from the middle

toward the periphery. The following spring the maple, elm, and Euonymus bush showed no signs of life. The lindens produced foliage, but the leaves were bleached and smaller than usual. Dried cambium and a rich growth of fungi were further indications of injury.

Similar investigations were carried on by SPÄTH and MEYER (**4**). In one case during the summer a little less than $1^{cu.m}$ of gas diffused daily through $17.8^{cu.m}$ of soil in a wooded plot. The roots of all the trees were killed within a few days. During four winter months the same amount of gas was allowed to escape into a wooded plat of twice the above area. In this case Platanus, silver poplar, American walnut, and Ailanthus were killed; the maple and horse chestnut were greatly injured; while the linden showed no injury. In another experiment $0.0185^{cu.m}$ of gas was daily distributed equally among seventeen trees. The experiment lasted from April 11 to June 27. Before May 30 six of the more sensitive trees had died. By June 21 all the others, with the exception of the rough-fruited maple, had slackened their growth. The leaves of the injured trees were a pale green or yellow, and most of the younger roots were dead. According to the statement of the gas inspectors, their methods were not capable of detecting such light leaks as are shown in this experiment. These investigators found that when the surface of the soil is compact, the gas may travel long distances before reaching the surface. An instance is cited of gas traveling from a leak on one side of a street to a cellar on the opposite side, where it became evident by an unbearable smell. These investigators concluded that trees are far less sensitive to gas leaks during the winter than during the growth period. They also found much more rapid injury where the surface of the soil was packed. The small quantity of gas necessary to kill and the great distance that gas travels through the soil serve to emphasize the danger to which trees are exposed.

H. EULENBERG (**5**), besides summarizing the results given in previous literature, adds the birch to the list of less sensitive trees.

J. BÖHM (**6**) grew slips of water willow in water through which gas was passed. He found that they produced only short roots and that these soon died, as did also the buds. The twigs themselves remained alive for about three months, until, as he believes, the

reserve food had been exhausted. In another experiment he found that soil impregnated with gas was very poisonous to plants, for seeds put to germinate in it started, but their roots soon died. A Dracaena planted in such soil died in ten days. Far less injury was shown when a given quantity of gas was in contact with the portions of the plant above the ground than when the same quantity came in contact with the roots by being passed into the soil. The roots, he concludes, are most sensitive to gas injury. He found potted plants of Fuchsia and Salvia only moderately sensitive to illuminating gas that was allowed to bubble through the soil.

LACKNER (**7**) states that camelias, azalias, cacti, and ivy are much injured if kept in rooms where illuminating gas is burned; while palms, dracaenas (*Acuba japonica*), and many other plants escape uninjured. He asserts that it remains to be determined whether it is escaping portions of unburned gas or products of incomplete combustion that produce the injury.

C. WEHMER (**8**) calls attention to a severe case of gas poisoning in Hanover. Thirteen elm trees along a street showed injuries varying with the distance they stood from a leak in a gas pipe. In late winter a number of them showed brown discoloration of the inner bark, and a falling-off of bark in large patches extending up the trunk six feet from the ground. No blue discoloration of the roots appeared as was reported by KNY and other observers. The author asserts that the area of the injury was especially great because of the hard-packed street above the leak.

MOLISCH (**9**) found that illuminating gas is more injurious to the roots of plants than chlorin or carbonic acid. Growth in length is retarded by 0.005 per cent. of illuminating gas. If uninjured and decapitated roots of corn are grown in illuminating gas, the former are remarkably bent and retarded in their growth in length, while the latter grow almost straight and are comparatively vigorous. Under the influence of the gas the growth in thickness of the roots is increased, the greatest thickening occurring where the bending is sharpest. When a 10–20 per cent. mixture of illuminating gas exerts a stimulus from one side, the roots respond negatively.

NELJUBOW (**10**) notes some very interesting effects of illuminating gas upon the etiolated seedlings of peas and other legumes. WIESNER

had already reported a horizontal nutation of these seedlings, which he explained as autonomic. RIMMER later explained this horizontal growth as a response to unfavorable conditions, especially lack of moisture in the air. NELJUBOW found that while this response always occurred in the dark in the laboratory air, it did not occur in the dark in a greenhouse or in the outside air. After determining that temperature and moisture were not factors, he sought the explanation in impurities of the laboratory air. He found that laboratory air passed through KOH, $Ba(OH)_2$, $CaCl_2$, red hot CuO, and finally through $Ba(OH)_2$ gave vertical seedlings; while similar treatment with the CuO unheated gave seedlings with the horizontal placement. This proved that some impurities (probably some of the constituents of illuminating gas) of the laboratory air, which were oxidized by glowing CuO, caused this peculiar horizontal placement. He later produced the effect with mixtures of illuminating gas. He likewise tested a number of the constituents of illuminating gas. Acetylene produced this nutation, but was difficult to work with, because, on the one hand, a slight increase in concentration killed, and on the other, it rapidly disappeared because of its high solubility in water. One part of ethylene in 1,000,000 of air gave the response, while one part in 4000 killed the majority of the seedlings. He likewise mentions the fact that various other constituents (benzene, sulfur dioxid, hydrogen sulfid, and carbon bisulfid) of illuminating gas are highly toxic. He makes no attempt, however, to determine the toxic limits of the several constituents, or to learn whether one or several determine the toxic limit of illuminating gas.

SHONNARD (**11**) mentions several manifestations of the injury of illuminating gas to trees, and describes an experiment with a potted lemon tree exposed to a flow of $1.07^{cu.ft}$ of gas per hour. After eight days he notes the exudation of sap in considerable quantity from trunk and branches, as well as the discoloration and falling-off of the leaves.

RICHARDS and MACDOUGAL (**12**) tested the effect of carbon monoxid and illuminating gas upon various seedlings. Carbon monoxid, heretofore considered neutral, was shown to be toxic. It was not so effective as illuminating gas, however, in modifying the rate and amount of growth of root and shoot, in retarding the differ-

entiation of the primary tissue, and in hindering the formation of chlorophyll. Gametophytes of certain mosses were found to be very resistant, suffering very little injury in high concentrations of these gases for three months. A more delicate moss, presumably *Mnium undulatum*, however, showed deleterious effects earlier. In Elodea and Nitella older cells were most injured, and the injury was shown by plasmolysis of the cells. A considerable part of their experimentation with illuminating gas serves to confirm the results obtained by MOLISCH, NELJUBOW, BÖHM, and others. The conclusion that "illuminating gas affords, in addition to the action of carbon monoxid, the results of the action of other substances deleterious to plants" seems to indicate that the work of NELJUBOW and others was entirely overlooked.

STONE (**13**) calls attention to the fact that very small leaks (2–3 cu. ft per day) of gas may cause local injury to trees. Among manifestations of gas-killing in trees, he notes the early appearance of an abundant growth of fungi in contrast to the relatively late appearance on other dead trees. In speaking of the distance gas may travel he says: "In gravelly soils we have known gas to travel 2000 feet without difficulty, when the ground is frozen, and escape into the cellar of a house; whereas in heavier soils gas is more likely to be restricted to smaller areas."

RICHTER (**14**) and other investigators have pointed out a number of effects of impurities of laboratory air upon the responses of seedlings. RICHTER believes that in a number of cases the negative geotropism of hypocotyls is greatly weakened by these impurities. He points out that a one-sided illumination will produce far more nearly a horizontal position with than without these impurities. He likewise asserts that in many species the degree of horizontality from one-sided illumination indicates the degree of impurity of the air. He found great variation, however, in sensitiveness in different species even of the same genus.

2. Scope, method, and preparation of material

It is quite commonly asserted that plants do poorly in houses lighted with gas and especially is the flowering interfered with. Various inquiries have come to us from carnation growers as to the

effect of illuminating gas upon the flowering carnation. These growers claimed to have had heavy losses from gas that seeped from defective pipes through the ground into the greenhouses. In some cases it is claimed that the losses occurred during cold weather, when little ventilation was possible and when the ground was frozen, so that upward diffusion from the defective pipes was hindered and thereby lateral diffusion fostered. In all these cases it is claimed that the injuries ceased with the repair or removal of the pipes.

Upon looking up the literature it was found that no accurate determinations were made upon the effects of illuminating gas and its constituents upon flowers, and that in no case have the toxic limits and relative toxicity of the several main constituents been determined. In short, it is not known in any case whether the toxic limit of the gas is determined by the action of one constituent or by the combined action of several. To answer these questions is the purpose of the investigation here reported.

This paper will deal entirely with the buds and flowers of the carnation, describing in detail the effects and toxic limits of illuminating gas and ethylene. A later paper will give in detail similar data for the other main constituents of illuminating gas, as well as describe the effects of illuminating gas and all its main constituents upon the vegetation of the carnation. The work naturally falls into these two divisions, for, as will be shown by experiments described later, the flowers are far more sensitive to illuminating gas than is the vegetation, and the toxic limit of the gas on the flowers seems (from all the evidence of our experiments) to be entirely determined by the ethylene it contains.

To determine the relative sensitiveness of buds and flowers on the one hand, and the vegetation on the other, as well as the relative sensitiveness of buds and flowers of different ages, one series of experiments was carried on by exposing entire potted plants to an atmosphere containing small proportions of gas. This was done by setting the plants into an air-tight greenhouse within the laboratory greenhouse, and then running desired quantities of gas into the air-tight greenhouse. This sort of experiment has some serious faults. It does not determine whether the flower is affected directly by the gas contained in the air about it, or whether the effect is indirect by

injury to the plant through the absorption of gas by the soil and later by the roots. Also no definite determination of the toxic limit of the gas can be made, for the amount absorbed by the soil is not determinable.

To avoid such sources of error the buds and flowers still intact were exposed individually to the desired concentrations of the gases. This was accomplished by the use of the apparatus shown in *fig. 1.*

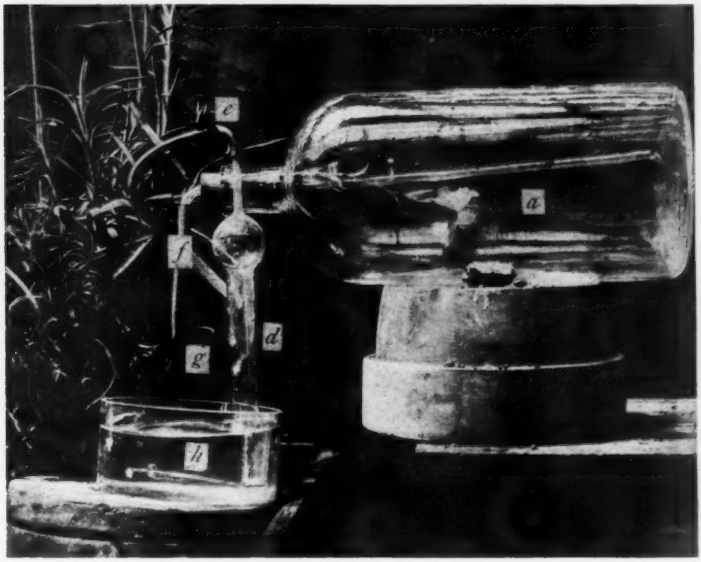


FIG. 1.—For description see text.

The bottle *a* is furnished with a three-holed rubber stopper. In one hole of the stopper is a straight glass tube reaching nearly to the bottom of the bottle. A calcium chlorid tube (*d*) is attached to the projecting end of this tube by means of a rubber tube furnished with a pinchcock (*e*). In the second hole of the stopper is a short bent glass tube (*f*), the outer end of which is furnished with a rubber tube and pinchcock (*g*). The third hole in the stopper is small and is capable of having the stem of the carnation inserted from the side by a split, which reaches from the hole to the margin of the cork. In setting

up the experiment the cork is placed on the stem of the carnation by opening the cork at the split and inserting the stem. The flower or bud and the long tube are put into the nozzle of the bottle and the cork forced in until the whole apparatus is air-tight. The free end of the calcium chlorid tube is placed into a dish (*h*) of water or (with gases highly soluble in water) mercury; both pinchcocks (*e* and *g*) are opened; and suction applied to the tube *f* until the liquid rises to the small portion of the calcium chlorid tube, at which time pinchcock *g* is closed. The desired quantity of gas which is now poured into the wide end of the calcium chlorid tube rises to the top of the liquid. A one-holed rubber stopper, furnished with a tube and attached to a column of the same liquid as is contained in the dish, is now inserted into the free end of the calcium chlorid tube (*d*), and the pressure of the column allowed to force the liquid to the inner end of the long tube. This forces the gas into the end of the bottle farthest from the flower and allows a gradual distribution by diffusion. For ethylene and illuminating gas water was always used as the forcing liquid.

In determining the toxic limits of illuminating gas and ethylene, 20-liter carboys were used; while smaller bottles were employed in some of the earlier experiments with these gases, as well as with all the determinations of the least toxic gases. The question of the effect of corking a bud or flower in a closed chamber of this kind naturally arises, and suggests a criticism upon the method. It was found that flowers opened without any apparent injury when corked in flasks of only one liter capacity. In all checks and in all cases where the concentration of the injurious gas was below the toxic limit, the flowers bloomed normally while yet in the bottles. To avoid undue rise of temperature within the chambers basket-covered carboys were used. The experiments were carried on in the laboratory greenhouse during the months of May to September. The temperature in the experiments reported varied from 20°–28°, and within this range no noticeable variation in toxicity appeared.

Two varieties of carnations were used—the Boston Market and the pink Lawson. The two varieties vary so little in their sensitiveness and reaction to ethylene and illuminating gas that a description of the responses of one applies equally well to the other.

To make sure that the effect produced by ethylene was not due to some impurity contained by it, parallel experiments were run with ethylene derived by two different methods: (1) by heating concentrated sulfuric acid with absolute alcohol, and (2) by dropping absolute alcohol upon phosphorous pentoxid heated to 200° C. and later raised to 240° C. The ethylene derived from sulfuric acid was washed by the ordinary gas burette and pipette, as described by HEMPEL (**15**: 34–95); first in concentrated sulfuric acid (sp. gr. 1.84) to remove the aldehyde, and later in 33 per cent. potassium hydrate to remove the sulfur dioxid. In each case the washing was continued until no further absorption occurred. The ethylene derived from phosphorous pentoxid was washed similarly, and in addition in copper sulfate (sulfuric acid solution described by HEMPEL, p. 316) for absorption of phosphene, if any should be present. Various samples of the ethylene derived in this way were analyzed. Bromin and fuming sulfuric acid absorbed 96–98 per cent. The unabsorbed portion proved to be air, coming from the generator chamber. The gases thus derived were diluted with air to form mixtures containing 2 per cent. ethylene. The toxicity of the two mixtures was equal.

In discussing the composition of illuminating gas we can hardly do better than quote a paragraph from SMITH'S (**16**) *General chemistry for colleges:*

> The illuminating gas in Europe, and in many of the smaller cities of the United States, is usually coal gas; while in the larger cities of America it is almost always made from water gas. Coal gas is obtained by the destructive distillation of soft coal, and is freed from ammonia and tar by washing and cooling, and from hydrogen sulfid and carbon dioxid by passage through layers of slaked lime. The water gas, made by the action of steam upon anthracite or coke, being composed of carbon monoxid and hydrogen, has no illuminating power. It is therefore "carburetted," that is, mixed with hydrocarbons, by passage through a cylindrical structure filled with white-hot firebrick, upon which falls a small stream of high-boiling petroleum. The relatively involatile hydrocarbons of which the oil consists are thus decomposed ("cracked"), and gaseous substances of high illuminating power are produced. The following table shows the composition of each of these kinds of gas, together with that of oil gas (Pintsch's) which is composed entirely of the products from "cracking" oil:

Components	Coal gas	Water gas	Oil gas
Illuminants	5.0	16.6	45.0
Heating gases:			
Methane	34.5	19.8	35.8
Hydrogen	49.0	32.1	14.6
Carbon monoxid	7.2	26.1	....
Impurities:			
Nitrogen	3.2	2.4	1.1
Carbon dioxid	1.1	3.0	....
Candle power	17.5	25.0	65.0

These are average numbers, and considerable variations from these proportions are often met with. The illuminants are unsaturated hydrocarbons, such as ethylene and acetylene, and the value of the gas for illuminating purposes depends on the amount of these particular components.

The illuminating gas used in our experiments was water gas of the People's Gas Light and Coke Company, drawn from a tap in the Botanical Laboratory. In numerous analyses of samples of this gas (see HEMPEL, p. 282) absolute alcohol absorbed 0.2–0.6 per cent., and fuming sulfuric acid 11–14 per cent. Absolute alcohol absorbs the so-called hydrocarbon vapors (mostly benzene); and fuming sulfuric acid the heavy hydrocarbons, including acetylene, ethylene, and their higher homologues. Bromin is often used as an absorbent of ethylene. Besides ethylene, however, it absorbs several other constituents of illuminating gas. In a number of analyses this reagent absorbed 9–13 per cent. A more definite determination of ethylene will be given in the experimental portion.

At first the illuminating gas used was washed through 33 per cent. potassium hydrate to absorb any traces of sulfur dioxid and hydrogen sulfid it might contain. This was found not to modify the toxicity, and hence the unwashed gas was used thereafter. The methods of deriving and purifying the other constituents (of illuminating gas) worked with will be described in the later paper, which gives their effects.

3. Experimental

ILLUMINATING GAS

As a later paper will deal fully with the effects and toxic limits of the constituents other than ethylene, we need make only a general statement concerning them here. A number of experiments were run

to determine the toxic limits of methane, carbon monoxid, acetylene, hydrogen, carbon bisulfid, and benzene to the buds and flowers. As would be expected, hydrogen was perfectly neutral when it completely displaced the nitrogen of the air. In all the other constituents here mentioned, the toxicity was such that in the least amount of illuminating gas necessary to kill the bud no one is concentrated enough to reach $\frac{1}{50}$ of its toxic limit. It is very probable, therefore, that these constituents play no part in determining the toxic limit of illuminating gas. It has already been stated that the absorption of hydrogen sulfid and sulfur dioxid does not modify the toxicity of the gas. This leaves, then, ethylene, the higher homologues of ethylene and acetylene, and certain aromatic sulfur compounds to account for the toxicity of the gas. All these substances except ethylene exist in very small percentages in illuminating gas. All evidence in the following experiments also points to the conclusion that there is enough ethylene in the gas to account for its toxicity.

The small greenhouse in which entire potted plants were exposed to the action of gas had a capacity of $1.69^{cu.m}$. In order to make comparisons easy between buds of the same size on the plants exposed and on the checks, corresponding buds were tagged with the same numbers. We need describe only one of these experiments. Potted plants of the Boston Market were put into the small greenhouse in the evening and 2 liters of gas were run in at the end opposite the plants, allowing a gradual distribution by diffusion. The plants were taken out the next morning to prevent injury by high temperature. The following evening the plants were returned to the enclosure and left for 60 hours (the following two days being cloudy). At the time they were put in, 4 liters of gas were run in, and the same amount was added 48 hours later, there being at that time no perceptible smell of gas in the chamber. This experiment served to show (1) that the vegetation is far less sensitive to gas injury than the buds, for there was no apparent injury to the vegetation; (2) plants remained vigorous, put out new buds, and later produced other flowers. The oldest buds (those showing color and just ready to open) and the youngest buds (those less than 0.6^{cm} in diameter) were the ones most injured. Many of the medium-sized buds, however, escaped death, although retarded considerably in their growth. The older buds

showed a slight growth of the petals, but never opened. Later they shriveled and turned yellow.

FIG. 2.—*a*, result of treating a bud, just beginning to show the petals, for three days with 1 part of illuminating gas in 20,000; *b*, result of the treatment of a similar bud, for the same length of time, with 1 part of ethylene in 500,000.

Our experiments in which individual buds were enclosed and exposed to illuminating gas began with liter flasks in which as much as 25^{cc} of gas was used. The time of exposure was usually three days, starting when the petals were just beginning to show. A gradual reduction of the concentration by reducing the amount of gas used and by increasing the size of the enclosure finally located the toxic limit. The highest concentration did no apparent injury to the vegetation; but the effect upon the buds was made apparent by a failure to open, by a discoloration and withering of the petals, and by the projection of the stigmas. When using 1^{cc} of illuminating gas to 20,000^{cc}, the stigmas still project as shown in *fig. 2, a;* 0.5^{cc} of illuminating gas did not sufficiently retard the growth of the petals to cause projection of the stigmas, yet the buds never opened farther than shown in *fig. 3*, although the petals remained fresh for several days. Very young buds were also exposed to the last concentration of the gas (1 part in 40,000, or 0.0025 per cent.) for a period of three days. The injury was not apparent at first, and the buds remained green for several days, but finally turned brown and withered.

FIG. 3.—Result of treating a bud, just beginning to show the petals, for three days with 1 part of ethylene in 1,000,000.

A series of exposures was also made on the open flowers. We selected for this work those that had just opened, in order to be sure that any change produced was due to the toxicity of the gas rather than to the natural death of the flower. Here as well as in all the other experiments checks were kept. *Fig. 4, a* shows a flower before being corked in a 20-liter carboy; *b*, the same after being

corked in a 20-liter carboy (containing air only) for 24 hours; *c*, a flower before being corked in a 20-liter carboy; and *d*, the same after being corked in 12 hours with 0.5^{cc} of illuminating gas. This shows that 0.5^{cc} of illuminating gas per 20,000 (1 part in 40,000) causes the complete closing of the flower in 12 hours or less. Higher concentrations caused a more rapid closing and a marked inrolling of the petals. With 0.5^{cc} per 20,000 and less the inrolling is not conspicuous. Even 0.2^{cc} per 20,000 causes considerable closing in 12 hours, though not as marked as 0.5^{cc}.

The effect of duration of exposure was also tested. No injury was done to a bud just ready to open upon one day's exposure to 2^{cc}

FIG. 4.—*a*, a flower that has just opened; *b*, the same after being corked in a 20-liter flask of air for 24 hours; *c*, a flower that has just opened; *d*, the same after being exposed 12 hours to 1 part of illuminating gas in 40,000; *e*, result of treating a flower that just opened for 12 hours with 1 part of ethylene in 2,000,000.

of gas per 20,000 (four times killing concentration for three days' exposure). On a similar bud 5^{cc} for one day was considerably more injurious than 0.5^{cc} for three days. The stigmas did not project, but the petals were markedly discolored.

During the entire period of experimentation there was no very marked variation in the toxicity of the gas used.[1]

[1] In determining the toxic limits we located a concentration that produced the effect while one-half that concentration did not. It is clear that this permits considerable va iation without detection. It is not possible to locate the toxic limits more closely, due to the variation in the flowers. It is clear, however, that this gives a very good idea of the magnitude of toxicity.

ETHYLENE

The experiments with ethylene were begun by exposing buds just beginning to show the petals to 1, $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, and $\frac{1}{16}$ cc of ethylene in 20 liters.

In each of these concentrations the buds were killed on three days' exposure. The usual signs of gas poisoning were noted; petals turned yellow and withered, and the stigmas projected. Since it was evident that these concentrations were far above the toxic limit, we resorted to the use of a 2 per cent. mixture of ethylene with air. Various amounts of this were used, until the toxic limits were definitely located. With 2 cc of this 2 per cent. mixture in 20,000 (1 part in 500,000), the results were similar to that obtaining with 1 cc of gas per 20,000 (1 part in 20,000). In *fig. 2, b* is a bud just showing the petals exposed to this concentration of ethylene for three days. Also 1 cc of 2 per cent. ethylene per 20,000 (1 part in 1,000,000) gives results similar to that shown by 0.5 cc of illuminating gas per 20,000 (1 part in 40,000). *Fig. 3* shows the results of such an exposure for three days on a bud just showing the petals. The growth of the petals is not sufficiently retarded to make the stigmas conspicuous; the petals remain fresh for several days but never open farther. Where much less than 1 cc of 2 per cent. ethylene per 20,000 was used with similar buds, three days' exposure did not prevent their opening.

When open flowers were exposed to the ethylene, it was found that 0.5 cc of the 2 per cent. mixture in 20,000 (i e., 1 part in 2,000,000) caused the closing within twelve hours. The result of such an experiment is shown in *fig. 4, e*.

It is seen from the data given above that ethylene must form approximately 4 per cent. of illuminating gas to be the constituent that determines the toxicity of the latter. It becomes necessary now to get an estimate of the fraction of the illuminating gas used that is ethylene. We have already stated that no absorbent used in gas analysis absorbs ethylene alone. In a special absorption chamber, packed in ice, 50 or more grams of bromin with 150 cc of water were placed, and measured quantities of illuminating gas passed through. When the bromin water was partially discolored, showing an almost complete exhaustion of the bromin, the resulting oil (a mixture of ethylene dibromid and other compounds resulting from the reaction

of the gas constituents with bromin) was separated, washed with a weak solution of potassium hydrate, and later with distilled water. This oil was then dried with fused calcium chlorid and later fractionated. In the first distillation all the portion boiling between 129° and 134° C. was saved. This was later redistilled and the fraction boiling between 103° and 132° C. saved as representing the ethylene dibromid, since this compound boils at 131° C. About 3 per cent. of the dried material absorbed by bromin boiled between 130° and 132° C.; a small portion boiled at 129° C. or below. From this it rose up quickly to 131° C., where it again gave a considerable fraction. Then it rose rapidly to 139° C., where a considerable fraction distilled. In one trial, 208 liters of gas at 27° C. and under pressure of 745.5^{mm} of mercury gave 130^{gm} of dried oil; of this 44.2^{gm} boiled between 130° and 132° C. After correcting for pressure and temperature the following equation equals the percentage volume of gas that is ethylene:

$$\frac{22.4\times760\times44.2\times300}{208\times745.5\times178\times273}=2.9+ \text{ per cent.}$$

In a second determination 138 liters of gas at 27° C. and 745.5^{mm} pressure gave 31.6^{gm} of oil boiling between 130° and 132°. Correcting for temperature and pressure, the following equation gives the percentage volume of ethylene in this case:

$$\frac{22.4\times760\times31.6\times300}{138\times745.4\times178\times273}=3.2 \text{ per cent.}$$

It must be stated, however, that according to WINKLER (**17**) the absorption of ethylene by bromin is not complete, and farther that considerable ethylene dibromid is necessarily lost in washing, drying, and distilling, so that the percentage is probably considerably higher than here obtained. It must be urged also that the presence of other oils with boiling points rather near that of the ethylene bromid tends to make this fractionation less accurate.

4. General

It is of great interest to know that the most delicate chemical test for illuminating gas in the atmosphere falls far short of detecting amounts that work havoc with the flowers of the carnation. The tests for carbon monoxid are those used for detecting illuminating

gas. The most delicate application of the blood test (see HEMPEL, p. 225) will detect 1 part of carbon monoxid per 40,000. The iodine pentoxid test (see HEMPEL, p. 226) is of equal delicacy. If carbon monoxid forms 25 per cent. of illuminating gas, these tests will detect 1 part of illuminating gas in 10,000. Upon three days' exposure 1 part of illuminating gas in 40,000 kills the young buds and the petals of the flowers just beginning to open; while 1 part in 80,000 causes open flowers to close upon an exposure of twelve hours.

The so-called "sleep" or closing of the carnation is a source of considerable loss to growers and dealers, for flowers that once close never again open. This "sleep" is especially likely to occur with cut flowers brought into city markets. Some varieties are so disposed to react in this way that their cultivation has almost entirely ceased. We know several homes lighted with gas where cut carnations can be kept only a few hours without "going to sleep." In one instance the displacement of gas lights by electric lights entirely overcame this difficulty. Our experiments show clearly that one cause of this sleep is traces of illuminating gas (ethylene) in the surrounding atmosphere.

STONE (**13**), WEHMER (**8**), and others have shown that illuminating gas diffuses great distances through the soil, especially if there is a hard-packed or frozen crust over the top. This paper shows the extreme sensitiveness of the carnation to this substance. From these facts it is evident that carnation growers whose greenhouses are in the region of gas pipes must take great precautions against losses from this source. It would be interesting to know whether solid cement walls set into the ground for some depth on the side next the pipes would furnish sufficient protection against leaks of this kind. It is clear that, if (as our results seem to indicate) the group of illuminants, or more accurately if one constituent of this group (ethylene) determines the toxicity of illuminating gas, coal gas is considerably less toxic than water gas, while oil gas is more toxic than either of the others; also the toxicity reported by the German investigators who used coal gas is less than that shown by the gas of the great American cities.

While it seems probable that the limit of toxicity of illuminating gas on the flower of the carnation is determined by the ethylene it

contains, it does not follow that such is the case with all parts of plants or even with the flowers of all plants. It would be interesting to know the effects and toxic limits of illuminating gas and its constituents upon various double as well as single flowers. Similar data for the foliage of various plants such as Coleus, which is supposed to be especially sensitive to illuminating gas, would likewise be of interest.

5. Summary

1. The flowers of the carnation are extremely sensitive to traces of illuminating gas in the air.

2. With the Boston Market and pink Lawson three days' exposure to 1 part in 40,000 kills the young buds and prevents the opening of those already showing the petals. The buds of medium age are considerably more resistant.

3. In the same varieties 1 part in 80,000 causes the closing of the open flowers upon twelve hours' exposure.

4. This injury takes place directly on the bud or flower exposed and not indirectly through absorption by the roots.

5. No chemical test is delicate enough to detect the least trace of illuminating gas that will cause serious injury to carnations.

6. The "sleep" of the carnation is probably often caused by traces of illuminating gas in the air.

7. Ethylene is even more fatal to the flowers of the carnation.

8. Three days' exposure to 1 part in 1,000,000 prevents the opening of buds just showing the petals.

9. Twelve hours' exposure to 1 part in 2,000,000 causes the closing of flowers already open.

10. There is much evidence that indicates that the toxic limit of illuminating gas upon these flowers is determined by the ethylene it contains.

The University of Chicago

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FLORAL SUCCESSION IN THE PRAIRIE-GRASS FORMATION OF SOUTHEASTERN SOUTH DAKOTA

SEROTINAL AND AUTUMNAL FLORAL ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 117

LEROY HARRIS HARVEY

(WITH FOUR FIGURES)

Serotinal floral aspect

Climatologically and florally the serotinal is perhaps the most distinctly demarked of the aspects. The climatological changes which set it off from the estival are quite generally appreciated, while the general blooming of the pioneer sod-formers during the early part of July with the accompanying serotinal bloomers no less distinctly marks it in a floral way.

One records now less dissimilarity in aspect and tone on crest, slope, and base; the more open association, however, still marks the crest. The tone is determined by the dull-greenish vegetative stalks of *Solidago rigida* and *Helianthus Scaberrimus*, which occur copiously throughout the formation. It is relieved locally on lower slopes by the yellow of *Ratibida columnaris* and on upper slopes by the blue of *Verbena stricta* and the canescence of Amorpha; while *Meriolix serrulata*, *Brauneria pallida*, *Potentilla Hippiana*, *Erigeron ramosus*, *Polygala alba*, and *Euphorbia marginata*, all of which extend over from the estival, are less influential. A few conspicuous forms are added in this aspect, but never of sufficient abundance to strongly variegate the dull green of the tone given by the leafy stems of Solidago and Helianthus.

The general flowering of *Agropyron occidentale*, *Bulbilis dactyloides*, and the Boutelouas, together with *Kuhnistera purpurea* and *K. candida*, distinctly marks the inception of the serotinal aspect, which is characterized by the gradual appearance of few but conspicuous bloomers and the attainment of maximum flowering of late estival forms, rather than by the addition of numerous forms as in the

SEROTINAL CLIMATOLOGY

Temperature	Maximum	37 C.
	Minimum	11 C.
	Mean	24 C.
Wind	Prevailing direction	S.
	Total movement	5682
	Hourly velocity	7.7
Rain	Days	10
	Mean daily	.25cm
	Total	7.95cm
Light	Mean cloudiness	3.8
	Sunshine per cent.	62
	Relative intensity	.604
Soil	Mean holard	12.4%
	Mean echard	7.2%
	Mean chresard	5.2%
Mean relative humidity		56.8
Relative evaporation		7.983

vernal and estival aspects, only thirteen new forms appearing during the aspect. It is moreover the aspect of the sod-formers, "floral" forms being represented by only six species. Several ruderals make their floral appearance in the formation during this aspect but, with the exception of *Cassia chamaecrista*, attain no conspicuousness.

The serotinal is markedly a period of extremes, bringing about a change to which one is generally sensible. During the early days of July the weather settles and there is a long succession of long and intensely hot and dry days, which condition characterizes the entire serotinal aspect. Relative evaporation (table) is at an extreme, though slightly less (0.81) than in the estival, finding its explanation in the lower (0.4) hourly wind velocity and higher (8.5) relative humidity; the hot dry winds from the south and southeast are now coexistent with the highest mean temperature, the lowest mean daily precipitation, a low relative humidity, and a high light intensity. Thus evaporation and transpiration are augmented to a precarious degree.

The chresard shows a continued decrease from the estival, being 6.5 per cent. on July 6 and 4 per cent. on July 24; while the average chresard is 5.2 per cent., the lowest yet reached. The holard of crest (8.2 per cent.), slope (12 per cent.), and base (12.2 per cent.) are now (July 28) more nearly approximate than in earlier aspects.

Relative evaporation at a maximum and

the chresard at a minimum are thus the ecological conditions which strongly mark the serotinal floral aspect.

SPECIES OF THE SEROTINAL FLORAL ASPECT

FACIES.—Bouteloua oligostachya,† B. hirsuta,† B. curtipendula,† Bulbilis dactyloides.*†

PRIMARY SPECIES.—Kuhnistera purpurea,† Verbena stricta,*† Ratibida columnaris,*† Kuhnistera candida,† Symphoricarpus occidentalis,*† Amorpha canescens.*†

SECONDARY SPECIES.—Agropyron occidentale, Carduus undulatus,* Euphorbia marginata,* Hymenopappus filifolius, Calamovilfa longifolia, Polygala alba.*

TERTIARY SPECIES.—Lygodesmia juncea, Lacinaria squarrosa, Brauneria pallida,* Meriolix serrulata,* Eriocarpum spinulosum, Erigeron ramosus,* Potentilla Hippiana.*

RUDERAL SPECIES.—Cassia chamaecrista, Onagra biennis, Amaranthus graecizans, Melilotus alba,* Chenopodium album, Lactuca canadensis, Apocynum cannabinum.

*From previous aspect. †Forming associations.

Agropyron occidentale is the first of the serotinal grasses to bloom. It is a xerophytic bunch-grass and occupies prairie crests, where it occurs copiously, rarely even of facial rank. It is one of the pioneers of the bunch-grass stage and is associated with the Andropogons, passing with these forms as they give place to the Bouteloua and being entirely absent in the older and more mesophytic prairie. In transitional stages from the bunch-grass open association to the less xerophytic closed sod association, Agropyron remains not infrequently in subcopious abundance as a relict of the earlier condition. The rootstock is here an efficient mode of propagation.

The three grama grasses, *Bouteloua hirsuta*, *B. oligostachya*, and *B. curtipendula*, which head out during the early days of July, enter upon anthesis almost simultaneously with the beginning of the second week of July, as does also the buffalo grass, *Bulbilis dactyloides*. The Bouteloua are pioneer sod-formers, following only the buffalo grass, which as the pioneer sod-former encroaches upon the bunch-grasses, replacing them and preparing the way for the Bouteloua which invariably follow closely. To the west, where the rainfall is much less, Bulbilis is the prominent sod-former and is the fodder grass of the great cattle ranges west of the Missouri. In our region it occurs along the xerophytic exposures of the bluff line, and as a

xerophytic relict along the crest of prairie knolls, where it mingles with the gramas as they advance upon the bunch-grass stage, yet usually as a secondary element among these sod-formers. In our area, however, it is lacking.

Bouteloua hirsuta seems to be the pioneer of the gramas as they encroach upon Bulbilis, or upon the bunch-grasses where Bulbilis is absent, as is the case in our formation. It is in turn apparently

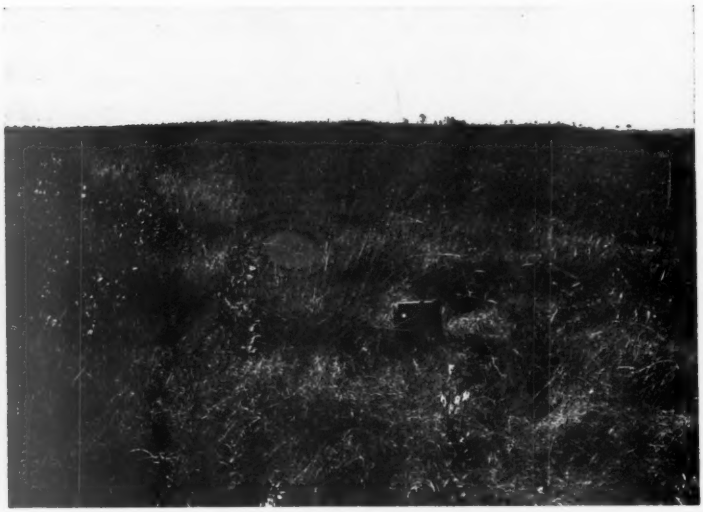

FIG. 1.—Serotinal aspect: *Bouteloua curtipendula* sod on upper slope; *Solidago rigida* to the left; *Helianthus scaberrimus* to the right; admixture in the background.

followed by *B. oligostachya*, which seems to occur more abundantly and to occupy the most prominent place of the sod-formers. Frequently it alone encroaches upon the bunch-grasses, *B. hirsuta* being absent. Next comes *B. curtipendula* (*fig. 1*), which also contributes largely to the early prairie sod. In many places the Poa sod is the next to follow. The gramas are thus largely confined to the crests, decreasing in abundance downward, where they not infrequently rise to facial prominence. Contrary to the serotinal floral forms, the Boutelouas are of low stature, *B. curtipendula* alone rising above

45^{cm}, which however may frequently reach 60 to 80^{cm}, and is the only species which becomes at all conspicuous. These species as they enter the open bunch-grass association form mats, which fusing form sod, finally resulting in the replacement of the bunch-grasses. The gramas are all perennial by means of the enlarged rootstocks.

Coincident with the flowering of the grasses is that of *Kuhnistera purpurea*, which seems to precede that of its related species *K. candida* by only a few days. The purple Kuhnistera is from its distribution and structure more xerophytic than the white-flowered species. The former occurs most abundantly on the higher slopes, decreasing in abundance downward; while the latter reaches its maximum abundance on the lower slopes, decreasing in the number of individuals per unit area upward. Along middle slopes the abundance of the two species approaches equality. Its distribution seems clearly related to the chresard of these various habitats. CLEMENTS ('**05**, pp. 233) in light of these facts has suggested the monophyletic origin of these two species from an ancestral form which became split up into *purpurea* and *candida* under the influence of and adaptation to a low and high chresard, a xerophytic and mesophytic habitat respectively, and has instituted experiments to test this theory. In their respective positions of maximum abundance each may rise to dominance, which, however, never occurs in the plot under study; the advanced condition of the prairie seemingly precludes such abundance in the closed association. However, they are the most conspicuous elements of the early part of the aspect. Their branching stalks rise 60 to 80^{cm} and are terminated by cylindrical spikes (some 8 or 9^{cm} long) of white flowers in *K. candida* and (some 5^{cm} long) of violet flowers in *K. purpurea*. They are perennials from thick and deep roots. The seeds are immobile, which with the perennial root accounts for their somewhat even distribution in the formation.

With the prairie clovers appear *Eriocarpum spinulosum* and *Lygodesmia juncea*. Eriocarpum is perennial from a deep woody root, whose much-branched stems rise about 30 to 40^{cm}, terminate in 1 to 25 heads fringed with yellow rays and 2.5^{cm} in diameter. In all it is very striking, but its rare occurrence along upper slopes and crests precludes more than a minor influence upon the tone. It

seems to demand only a low chresard, and upon more xerophytic crests than occur in our formation, where it holds its own, it appears copiously and not infrequently determines the tone of the open association. The wind-distribution is facilitated by a copious pappus. Perhaps no plant of our formation has the remarkable degree of adaptability possessed by *Lygodesmia juncea*. The first plant to appear upon the bare exposed soil of bluffs, it persists into a well-formed mesophytic sod with even a marked abundance. It is to be reckoned as a xerophytic relict in our plot, occurring most abundantly along the crest, but at most only sparsely. It is a perennial from a heavy woody root, which interprets its persistence in the formation, and this with its reduced scalelike leaves contributes to its fitness as a pioneer xerophyte. The much-branched stems (45^{cm} high) end in solitary pink-rayed flowers, whose small size and ephemeral duration never render them florally conspicuous. Distribution is very general and wide; the achenes are provided with a copious pappus.

During the last days of the second week and early in the third week of July the prairie thistle, *Carduus undulatus*, enters upon anthesis and florally characterizes this part of the aspect. Its densely white tomentose and much-branched stems rise some 90^{cm} and terminate in large (5^{cm} in diameter) solitary heads of numerous purplish flowers. It also assumes a gregarious habit, and patches occur here and there from base to crest of prairie slopes. Thus it is a most conspicuous form, but reaches its maximum flowering only in early August. Wherever the prairie sod has been disturbed it becomes almost exclusive in its occupancy. It is a biennial of slightly mesophytic tendencies and so appears more commonly on lower slopes. Its high fertility and copious pappus insure a wide distribution, easily explaining its very general occurrence.

The last form to be added in the aspect is *Lacinaria squarrosa*, which appears here and there upon upper slopes and crests. It is very xerophytic in nature, occupying a prominent place in the early stages of the bluff line succession, and is in our plot to be considered as a relict. It is not conspicuous and adds little to the tone, which is at this time rendered bizarre by several of the earlier forms now in their greatest floral display. Lacinaria is an erect (50^{cm}) perennial

herb from a tuberous structure, terminating in a spike bearing numerous heads of purplish flowers. The abundant plumose pappus assures a widespread distribution.

. Autumnal floral aspect

No marked climatological change is to be noted in passing from the serotinal to the autumnal aspect, but simply one of gradually decreasing favorableness. Hence the latter has been set off partly for convenience of discussion, though it seems more or less distinctly characterized by definite floral activity; yet possibly it might be more accurately designated as late serotinal. Beginning in early August and marked by the estivation of such very conspicuous forms as *Helianthus scaberrimus*, *Solidago rigida*, and the bunch-grasses (*Andropogon furcatus* and *A. scoparius*), it extends into early October, when vegetative activity comes to an end. Its floral activity is terminated, however, in middle September by the flowering of *Gentiana puberula* and *Solidago rigidiuscula*, while florally the aspect is at its best during late August and early September, when the prairie is a sea of yellow from the Solidagos, mainly *S. rigida*, dotted here and there by the blue of Asters. Rising sentinel-like along higher slopes and crests are the rose-purple spikes of the blazing-stars, while on isolated knolls associations of *Aster sericeus* with their purplish flowers and white tomentose leaves relieve the sea of yellow. The bunch-grasses impart a very characteristic tone to the higher and more xerophytic knolls.

In earlier aspects marked restriction of forms was noted, less apparent in the serotinal it is here scarcely evident. On the other hand there is a marked identity of the controlling species on base, slope, and crest, the entire formation presenting an unbroken and identical covering, undoubtedly to be associated with the noticeable equality of the chresard throughout these various situations.

Eighteen of the twenty-two forms (82 per cent.) are composites, and all but one of these (*Kuhnistera villosa*) are wind-distributed. Like the prevernals the autumnals are pronouncedly xerophytic, fitting into uncertain, that is unfavorable, ecological conditions, the former at the initiation, the latter at the decline of floral activity. Just as prevernals have come to possess the spring period of not

AUTUMNAL CLIMATOLOGY

Temperature			Wind			Rain			Light			Soil			Mean relative humidity	Relative evaporation
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Mean cloudiness	Sunshine per cent.	Relative intensity	Mean hoiard	Mean echard	Mean chresard		
36 C.	4 C.	20 C.	E. & N.W.	5771	7.8	15	.26cm	15.9cm	4.0	63	.607	10.5%	7.2%	3.3%	55.4	4.671

over-favorable conditions, in the same degree the autumnals claim possession of that less suitable period during the closing days of vegetative activity, and for similar reasons. Each group has been able on account of peculiar characteristics to work into and occupy these periods unsuited for plants of less xerophytic tendencies, as their periods of growth and reproduction fitted into these seasons of the year, extremes in each case, where the great majority of forms could not succeed. As floral activity is more definitely restricted than vegetative, which is largely accomplished in earlier periods, it is also evident that the problems of pollination and seed dissemination must have been no small factor in working out through selection the floral restriction of these forms.

The following species extend over from the serotinal aspect, but are rendered inconspicuous by the overtopping layer of a few autumnal species: *Verbena stricta*, *Carduus undulatus*, *Ratibida columnaris*, *Meriolix serrulata*, *Polygala alba*, and *Lygodesmia juncea*. They become less and less conspicuous as the period advances.

As ruderals we may note *Melilotus alba*, coming over from earlier aspects, *Lactuca canadensis*, and *Salsola tragus*.

Conditions here are but the continuation and accentuation, during the early part of the aspect at least, of those of the serotinal. The maximum conditions there noted become less pronounced toward early September, and toward the middle of the month pass gradually into those more settled conditions of early fall in which maturation is

so largely accomplished. However, the climatological conditions (table) of this aspect bear to its floral activity a relation analogous to that existing in the prevernal, and the forms here occurring seem in no less degree peculiarly adapted to the late seasonal conditions.

In August the wind is dominantly from the south and east, but in early September begins to swing to the northeast quadrant, where it remains until the prevernal, then swinging round again to the southeast. The average daily rainfall (0.26^{cm}) remains about the same as in the preceding aspect, though it falls on only 25 per cent. of the days, while in the serotinal it falls on 33 per cent. of the days. Relative humidity, sunshine per cent., and relative light intensity are noticeably similar in these two aspects, while relative evaporation has decreased almost a third. In the fact that the hourly wind velocity has increased only a tenth, and in the 4° C. fall in the mean temperature must be sought an explanation of this lowered evaporation.

SPECIES OF THE AUTUMNAL FLORAL ASPECT

FACIES.—Andropogon furcatus,† A. scoparius.†

PRINCIPAL SPECIES.—Solidago rigida,† Aster sericeus,† Helianthus scaberrimus,† Sporobolus brevifolius.†

SECONDARY SPECIES.—Solidago rigidiuscula,† S. missouriensis, S. nemoralis, Ratibida columnaris,*† Aster multiflorus, Artemisia gnaphaloides,* Verbena stricta,*† Carduus undulatus.*†

TERTIARY SPECIES.—Aster oblongifolius, Solidago canadensis,† Kuhnia glutinosa, Lacinaria scariola, Nabalus asper, Lygodesmia juncea,* Polygala alba,* Dysodia papposa, Grindelia squarrosa, Kuhnia eupatorioides, Lacinaria punctata, Gentiana puberula, Kuhnistera villosa, Meriolix serrulata.*

RUDERAL SPECIES.—Salsola tragus, Meliotus alba,* Lactuca canadensis.*

*From earlier aspect. †Forming associations.

During the early days of August four forms, destined later to become very conspicuous, make their floral appearance in the following order: *Solidago missouriensis*, *Helianthus scaberrimus*, *Solidago nemoralis*, and *S. rigida*. *S. missouriensis*, the first of the autumnal bloomers, occurs in subcopious abundance and most abundantly in the open association of the upper slopes and crests, where it is quite noticeable, though it never becomes a prominent feature of the tone because of its low stature and small panicles. It is distinctly xerophytic, as is evident both by its structure and distribution, and, as

might be inferred, passes as the open formation gradually becomes closed, never being present in a compact sod at the base of the slope.

Appearing with *S. missouriensis* comes *H. scaberrimus*. It occurs both more frequently and abundantly than the former and is distinctly less xerophytic, reaching its greatest abundance upon middle and upper slopes. Its rigid, rough, and little-branched shoots, rising some 1.5^{m} and terminated by a spreading corymb bearing

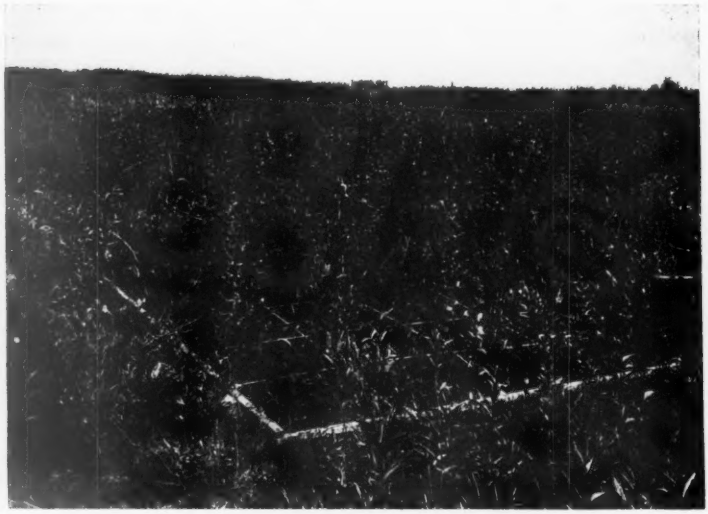

FIG. 2.—Late serotinal aspect: *Solidago rigida* and *Helianthus scaberrimus* on upper slope.

few conspicuous heads (3 to 5^{cm} wide) with numerous yellow rays, make it a conspicuous element of the early autumnal aspect, but it soon blends in the sea of yellow of *Solidago rigida*, which shortly comes on, completely dominating the floral tone. Helianthus (*fig. 2*) rarely holds its own along the tension line where the Poa sod is encroaching, but with other open association forms yields to its advancement, though it occurs inclusively in the less compact sods higher up the slopes, in which places it frequently assumes a copiogregarious habit. The stiff sunflower is perennial by a thick root-

stock. A very limited pappus of two to four scalelike awns provides only a restricted distribution, easily accounting for its gregarious tendency.

About a week or ten days later *S. rigida* begins its blooming, but only reaches its maximum about the last of the month, at this time solely characterizing the floral tone and maintaining a sea of yellow for some three weeks, when the tone begins to pale as fruiting advances and completely gives way during the third week of September, the bright-yellow floral tone yielding to the dull-green foliage. The stiff goldenrod occurs ubiquitously, but reaches its greatest abundance upon middle slopes, where it is frequently copious. The single stout stem (frequently several), from the perennial rootstock, rises somewhat over a meter, terminating in a flat dense cyme bearing numerous yellow-rayed flowers, frequently 20 to 25^{cm} across, which with its abundance and frequency makes *S. rigida* the most striking and dominating in its floral tone of any single species of the formation. Following the latter species by only a few days *S. nemoralis* comes into bloom. Overtopped by and much less abundant than the former, it never is conspicuous, though frequently it adds to the dominant yellow tone of the aspect. It reaches its greatest abundance on slopes, occasionally entering the open association of the crests, but is rarely included in the compact sod of lower slopes.

The three goldenrods just noted are alike perennial from a thickened rootstock, with a tendency toward the formation of perennial basal rosettes, and are widely wind-disseminated through the efficiency of the well-developed parachute.

Almost coincident with the blooming of these four forms is that of the bunch-grasses, *Andropogon furcatus* and *A. scoparius*. Though these two grasses during the last two aspects have been vegetatively conspicuous upon the higher crests and most xerophytic slopes, where they contribute the characteristic dull tone to the bunch-grass association, they flower only during the early part of August, thereby adding but little to their already established prominence. They are accompanied by *Sporobolus brevifolius*, which occurs less abundantly, but like the beard-grasses assumes the bunch habit upon higher crests and ridges. In these situations the Andropogons assume facial rank, *A. furcatus* (*fig. 3*) being the taller and on account of its

invariable bunch habit far the more conspicuous. *A. scoparius* (*fig. 4*) seems to form a very loose sod between the bunches of the former and extends lower down upon the slope, where in places it yields to the Boutelouas or rarely to Poa. In succession these forms seem to precede the Boutelouas. With a reduction of drainage and introduction of these sod-formers, the bunch-grasses yield, and in those portions of the prairie where succession has progressed most

FIG. 3.—Autumnal aspect: the bunch-grass, *Andropogon furcatus*, with intervening spaces occupied by Bouteloua sod near crest of prairie knoll.

rapidly, for example the northwestern exposure, the Andropogons and the "bunch-habit" are conditions of the past. With *Agropyron occidentale*, the Andropogons and Sporobolus must be ranked as the pioneer grasses of the prairie, and as such hold a most important ecological relation in the structure and development of the formation. *A. furcatus* yields first, giving way to *A. scoparius*, which in places assumes facial abundance and frequently persists in a somewhat anomalous way in the more mesophytic associations. These grasses

are wind-distributed, to which end the hairy awned spikelets contribute. Being perennials from heavy resistant rootstocks, they are well adapted to the precarious pioneer position they occupy in the formation.

Two composites, taking a minor place in the formation, must be mentioned. While belonging to the formation proper, they function mainly as ruderals. *Dysodia papposa*, which blooms at the beginning of the autumnal aspect and often earlier, occurs everywhere along

FIG. 4.—Autumnal aspect: an Andropogon sod, mainly *A. scoparius*, upon crest of knoll; scattered individuals of Solidago, Helianthus, and Aster are present.

roadsides and on wastes, where it attains its greatest size and abundance. Frequently on the most xerophytic of prairie hills and bluffs it assumes a very marked prominence. In our area it occurs subcopiously along crests and ridges, in fact anywhere that the association may be open, though it is usually depauperate in such cases. The fetid marigold is an annual, and its ubiquity finds cause in the ease and abundance of its dispersal through an efficient pappus, and in the period of its germination falling at the time when the majority of forms have long since germinated and the formation is thinning off its early annuals and prevernal and vernal perennials. To these

reasons must further be added its high degree of adaptability for germinating under these less favorable serotinal conditions.

The other form here included is *Grindelia squarrosa*, which occurs only sparsely and then almost entirely along lower slopes and frequently included in the Poa sods. On account of its scattered distribution, the gum plant usually grows about 50^{cm} high and branches much and more or less symmetrically, so that with its many heads of yellow ray-flowers it becomes quite noticeable in early September. Grindelia is a perennial from a heavy rootstock. The few awned achenes are inclosed in a glutinous head, consequently distribution is restricted, and correspondingly a gregarious tendency is to be noted.

During the last two weeks of August several forms of secondary prominence in the floral tone progressively bloom. They are *Solidago canadensis*, *Lacinaria scariosa*, *L. punctata*, *Artemisia gnaphaloides*, *Kuhnia glutinosa*, and *K. eupatorioides*. *Solidago canadensis*, the most mesophytic of our goldenrods, seems to be confined exclusively to Poa sods in valleys and at the base of slopes. It is here gregarious in tendency, occurring in isolated patches or clumps. Also upon disturbed soil around coyote burrows it usually establishes itself in dense patches. It rises about a meter, with several shoots from the same large perennial rootstock, branches profusely, bearing numerous heads in dense panicles, and in all is most conspicuous along with Grindelia at the base of slopes and in valleys. Its distribution by well-developed pappus is extensive, though its demands for the highest ecological conditions greatly restrict its establishment.

The two button-snakeroots, *Lacinaria scariosa* and *L. punctata*, bloom about the beginning of the last week of August, and though sparse in their distribution, being confined to crests, ridges, and the open association of upper slopes, they rise like sentinels of the prairie, relieving the blaze of yellow by touches of purple. *L. scariosa* seems more mesophytic than *L. punctata*, blooming usually a few days later and upon upper slopes mainly. It is also much taller and the heads are larger than in the latter and so more prominent. The numerous short-peduncled heads of purplish flowers, borne upon the erect unbranched and usually solitary stem from a prominent tuber, give these forms a most striking appearance. Copious pappus assures a wide wind-distribution.

The prairie mugwort, *Artemisia gnaphaloides*, is gregarious upon upper slopes. Here it forms dense patches, and these, on account of the white tomentosity of its stems and leaves, which are frequently 50^{cm} high, are conspicuous in the dominant tone of yellow. It bears to the autumnal quite the relation that the Antennarias hold to the prevernal and vernal tone. Perennial from a tuber-like root, it is also xerophytic in tendency. In its pappate achenes and root-propagation are found the causes of its gregarious habit.

The closing days of August are marked by the estivation of the two false bonesets, *Kuhnia eupatorioides* and *K. glutinosa*. They both occur but rarely and then mainly upon upper slopes and crests. They form little clumps (several shoots from the same perennial root) and are tall (50 to 75^{cm}) and much branched, but on account of their small few-flowered heads of creamy-white color and their only occasional frequence, they never attain any prominence. However, they become much more noticeable when the rich white pappus spreads in maturation, during the second week of September. *K. eupatorioides* is more mesophytic and so occurs more frequently over the formation. *K. glutinosa*, however, is pronouncedly xerophytic, and is restricted in its distribution to the open association along crests and higher slopes. The abundant barbulate pappus assures prolific invasion, though establishment seems to be very limited, doubtless due to the apparently low degree of adaptability possessed by these forms.

The Kuhnias are accompanied by *Nabalus asper*, which is restricted to lower slopes, is of rare occurrence and thus always a minor element. Though it is of the upper layer and bears numerous heads of pale-yellow flowers, it blends into inconspicuousness in the general tone. It is a perennial from a tuberous root. A well-developed parachute insures wide dissemination, but high ecological demands preclude more than a rare establishment upon the prairie.

The early days of September are well marked by the blooming of four forms which occasionally attain more or less restricted prominence: *Aster sericeus*, *A. multiflorus*, *A. oblongifolius*, and *Kuhnistera villosa*. They are all of evident xerophytic tendencies and occur mainly upon the upper slopes and crests. Appearing at a time when there is an apparent decline in the dominance of the earlier tone, and

occurring in the open association, the Asters become quite noticeable though they are all of a lower layer than *S. rigida*. The silky Aster, *A. sericeus*, usually of low abundance and general occurrence, frequently becomes copious on bunch-grass knolls, there forming very distinct associations. Rising some 50^{cm}, with numerous spreading branches terminating in prominent heads (2 to 3^{cm} in diameter) with numerous violet rays, and bearing abundant leaves which are densely covered above and below with a silvery-white silky pubescence, this Aster is always a conspicuous element of the middle and late autumnal aspect. Its achenes are equipped with a medium pappus. It is a perennial from a thickened rootstock.

The two other Asters are similar in frequency and abundance to *A. sericeus*, but never attain its prominence. Of these *A. oblongifolius* always occurs with *A. sericeus* in the open association. With us it always remains depauperate. Seldom more than 30^{cm} high, it is ever inconspicuous, though its bluish rays make it noticeable at short range, since it is usually overshadowed by *A. sericeus*. It is a perennial and is wind-distributed; a copious pappus serves to bring about a general invasion, which, as in the other Asters, seems to be coupled with a high percentage of establishment, especially in the open xerophytic associations of the formation. The dense-flowered aster, *A. multiflorus*, occurs perhaps more frequently but less abundantly than the former, and is similarly a xerophyte of the open association, in which situations it never reaches other than a reduced stature. However, its bushy spreading branches, thickly beset with numerous small white heads, invariably make it more prominent than *A. oblongifolius*, particularly when it occurs in patches. It seems to work down upon the lower slopes, here attaining a greater stature and abundance as well as a greater prominence in anthesis.

All the Asters are perennial from rootstocks and form small basal rosettes, and are wind-disseminated.

The hairy prairie clover, *Kuhnistera villosa*, is a perennial from a deep tuberous root. Densely silky pubescent, abundantly branched, and terminating in cylindrical clustered spikes (3 to 6^{cm} long) of rose-purplish flowers, it is in itself quite conspicuous, but its restricted frequency and rare abundance make it rarely a tonal component in the formation. In the bunch-grass formation it becomes, with *Amorpha*

canescens, more abundant but never controlling. It is distinctly xerophytic, and while largely of the open association, it may work down slopes into more favorable habitats.

During the middle days of September the last two forms of the prairie-grass association present their flowers, *Gentiana puberula* blooming a few days before *Solidago rigidiuscula*, the last form to bloom. The downy gentian occurs rarely and is largely restricted to middle and lower slopes, rarely if ever occurring along the xerophytic crests and ridges. Its terminal group of few large light-blue flowers are rendered unimportant as the plant is of short stature (30 to 40^{cm}) and so hidden. It is perennial from thickened roots, and wind-distributed, the seeds being widely winged. Its rarity therefore lies no doubt in its high ecological requirements, being somewhat mesophytic in its nature.

The last form of the prairie to bloom is *Solidago rigidiuscula*. Flowering as it does when *S. rigida* is passing into fruit, of copious abundance and high frequency upon upper slopes, occurring gregariously at times with several stalks (5 to 15) arising from the same perennial root, it is rightly named the "showy" goldenrod. It persists nearly to the middle of October, and is one of the last forms to pass into fruit, though accompanying it are the later flowers of Meriolix, Ratibida, Carduus, Polygala, and Lacinaria. It is widely wind-dispersed and establishment is quite general.

Post-floral aspect

By the second or third week in October the prairie forms of the autumnal floral aspect have all passed into seed, and the gorgeous yellow of *Solidago rigida* has given way to the somber brown of frosted leaves and stalks. While seed maturation and distribution in species of earlier aspects have been in progress during the subsequent aspects, the post-floral aspect, extending up into late November, is particularly characterized by this phase of plant life, yet dispersal may and does continue, but in a much more limited degree even during the winter season. The little fall of snow leaves the prairie bare the greater part of the winter, its tone being in no way modified; the post-autumnal appearance remains to characterize the prairie throughout the non-flowering period, and, as has already been pointed out,

extends up to and even dominates the prevernal and vernal floral aspects.

Summary of the structure of the formation

The formation is strictly of the prairie-grass type, its facies being determined mainly by six species: *Bouteloua oligostachya*, *B. curtipendula*, *B. hirsuta*, *Koeleria cristata*, *Andropogon furcatus*, and *A. scoparius*, to which must be added *Poa pratensis* in valleys and on lower slopes. The Andropogons are the main sod-formers of crests and ridges, while the Boutelouas characterize the higher slopes, working up to the crest and ridges. Koeleria seems to be more closely associated with the Boutelouas, occurring on middle slopes mainly. With these are associated three sedges and seven other grasses, which are all important as cooperating sod-formers, some of them ranking as primary species in the formation. We may mention *Carex pennsylvanica*, *C. festucacea*, and *Sporobolus brevifolius* as perhaps the more important of these. It is to be remarked that the sedges are all pre-estival, while the grasses are all estival or post-estival in their floral activity; the first facies to bloom is Koeleria in the estival aspect, while the Boutelouas are serotinal and the Andropogons autumnal.

Upon this facial background of grasses there progressively appear several conspicuous flowered forms of primary importance, which with numerous secondary and tertiary species serve to impart a bizarre aspect to the formation when considered as a whole and a kaleidoscopic shift with seasonal succession. In passing it is well to note that species primary in their own floral aspect may be of only secondary or tertiary importance when the formation is considered as a unit. Among these primary species we may note the ubiquitous *Antennaria campestris*; the Spesias and Sisyrinchium of middle slopes; *Amorpha canescens* upon upper slopes and ridges; Ratibida upon lower, and Verbena and *Erigeron ramosus* upon upper slopes; Symphoricarpus in valleys and on lowest slopes; the Kuhnisteras upon slopes, *K. purpurea* occupying the upper slopes, while *K. candida* extends downward upon lower slopes; *Solidago rigida* and *Helianthus scaberrimus* of great frequency and abundance; and finally *Aster sericeus* upon isolated knolls.

Among the more important of the secondary species may be mentioned *Viola pedatifida* and *Oxalis violacea* of middle and lower slopes; *Meriolix serrulata* of higher slopes; the Lithospermums of the more xerophytic portions of the formation; *Plantago Purshii* of middle slopes; *Linum rigidum* in the open association; *Potentilla Hippiana*, *Carduus undulatus*, and *Polygala alba*, which occur on middle and lower slopes; *Solidago rigidiuscula* and *S. nemoralis* upon lower and middle slopes, and *S. missouriensis* upon upper slopes mainly; and finally *Aster multiflorus* and *A. oblongifolia*.

Considering the ground association, the open association prevails over ridges and crests and extends down somewhat on slopes, passing gradually through a transitional condition into the closed association which occupies the valleys, depressions, and base of slopes, working always up or outward, displacing the open association. *Poa pratensis* establishes the most dense association, but the Boutelouas, Koeleria, and Festuca exert perhaps a more extensive influence in reducing the open association. In this connection it should be noted that the Andropogons are *par excellence* the pioneers, breaking up the xerophytic open association upon the highest and most xerophytic crests, preparing the way for the Boutelouas. It may be possible that in some cases the Andropogon bunch-grass stage was not the pioneer society, but that on account of more favorable soil moisture conditions, largely a question of drainage, the Boutelouas were the initial sod-formers. However, upon crests and ridges of excessive drainage the Andropogons have invariably preceded the Boutelouas and Koeleria. Occurring rarely in the open association is an undetermined xerophytic moss, while two species of the Basidiomycetes have been noted in the more mesophytic portions of the formation.

The enumeration of species includes 90 forms belonging to the formation proper and some 18 ruderals which work into the formation from the contiguous cultivated regions. The most abundant and prominent of the latter are *Cassia chamaecrista*, two species of Melilotus, *Hordeum jubatum* on lower slopes and moist soil; *Panicum capillare*, *Verbena bracteosa*, and *Amaranthus graecizans* of the more open associations; *Onagra biennis* of general occurrence; Salsola of the open association; and finally *Lepidium virginicum*, which not infrequently becomes quite abundant in the open association of

higher slopes. These ruderals are characteristically confined to marginal invasion, though they are frequently found wherever the open association makes possible their establishment. Onagra, however, is able to establish itself in the closed formation, as is *Potentilla monspeliensis*. Hordeum especially makes advance where some artificial agency has destroyed the equilibrium in rich moist stations; frequently in such cases it assumes even facial rank.

The 90 prairie elements proper have a most interesting taxonomic distribution. The composites with 29 species (32.2 per cent.) form the dominating family, comprising nearly a third of the total forms. The Gramineae number 15 species (16.6 per cent.), and though not leading in species they rank first in number of individuals. The third important family is the Leguminosae with 11 species (12.2 per cent.). Thus these three families provide 61 per cent. of the prairie elements and perhaps over 90 per cent. of the individuals. The remaining 35 species (39 per cent.) are conspicuous on account of their diverse affinities, belonging as they do to 22 different families, 14 of which have only a single representative in the formation. The families are as follows: Borraginaceae (4), Ranunculaceae (3), Cyperaceae (3), Onagraceae (3), Scrophulariaceae (2), Linaceae (2), Rosaceae (2), Oxalidaceae (2); and the following with one species each: Nyctaginaceae, Cruciferae, Umbelliferae, Iridaceae, Violaceae, Euphorbiaceae, Caprifoliaceae, Solanaceae, Labiatae, Plantaginaceae, Gentianaceae, Verbenaceae, and Polygalaceae.

The life conditions of the formation are by no means equable, and in this relation it is significant to record that only 11 per cent. of the species are annual, the majority of which produce abundant seeds and are provided with efficient means of distribution and occur mainly in the xerophytic open associations. Of the remaining 89 per cent. which are perennials, 96.2 per cent. are geophytic; Rosa, Symphoricarpus, and Amorpha alone are woody.

In a region characterized by strong prevailing winds it is to be noted that a high percentage of the species is wind-distributed. An analysis of this point shows that about 90 per cent. are so disseminated, some 55 per cent. showing especial facilities to this end. The great range of specific forms and their marked frequency in the formation finds an explanation in this permobility of repro-

ductive organs possessed by such a large percentage of its components.

As to pollination, 20 per cent. of the forms are wind-pollinated, while 80 per cent. have their pollen transferred by insects, the sedges and grasses comprising the former group.

Conclusions

1. The formation is a part of the Niobrara Prairie Region of CLEMENTS. In composition it is transitional. More truly a part of the prairie to the west, yet it contains several pioneer forms from the more mesophytic prairies to the south and east.

2. These two groups of elements during post-glacial migration have entered along two distinct lines of advance. The former migrated northwestward from a southwestern center of dispersal, while the latter followed a northwestern track up the Mississippi and Missouri valleys.

3. The prairie is pre-glacial in origin and is descended from the climatic prairie of Tertiary times, which arose in response to reduced precipitation caused by the upheaval of the Rocky Mountains at the close of the Cretaceous.

4. The climate is typically a prairie climate. A relatively dry resting season from October to March, in which only 16 per cent. (10.4^{cm}) of the total precipitation falls, and a moist growing season from March to September, in which 83 per cent. (49.31^{cm}) of the precipitation is distributed over sixty days, with 25 per cent. concentrated in April and May, insures a prairie formation. On the other hand, the annual low relative humidity, the dry and high winter winds accompanying high temperature, low winter rainfall, absence of a snow blanket, and the hot, dry summer of low precipitation are inimical to tree growth.

5. The absence of trees upon the prairie is primarily to be explained upon historical lines. The prairie was climatically determined and successfully and successively maintains itself against tree invasion from the edaphically determined arboreal fringes along flood plains and in ravines.

6. The northern slopes are the last to recover from winter, but are most mesophytic. It is up these slopes that the Poa sod and the

shrub association of Symphoricarpus and later *Rhus glabra* advance, preparing the way for the bur oak–slippery elm association, which likewise makes its greatest progress up these slopes from ravines and flood plains.

7. The floral activity of the formation may be approximately recorded in the following five aspects, set off by marked climatic and floral changes: prevernal, April 1 to April 25, 6 species; vernal, May 3 to May 31, 28 species; estival, June 1 to July 7, 21 species; serotinal, July 7 to August 7, 13 species; autumnal, August 7 to September 21, 22 species.

8. The prairie elements show a marked grouping into vertical layers, which correspond approximately with the floral aspects. Overtopped by the autumnal layer the sub-layers are successively those of the serotinal, estival, vernal, and prevernal.

9. There is a marked distinction in the chresard of base, slope, and crest in the prevernal, which becomes less marked in the subsequent aspects, approaching equality in the autumnal. As a result, the floral covering shows a corresponding difference upon base, slope, and crest in earlier aspects; the influence of position gradually declines, the floral covering presenting a striking similarity over the entire formation in the autumnal.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

A PARASITIC ALGA, *RHODOCHYTRIUM SPILANTHIDIS* LAGERHEIM, IN NORTH AMERICA

During February, 1908, Dr. F. L. STEVENS, of the North Carolina Agricultural College, sent me a few dried leaves of the common ragweed, *Ambrosia artemisiaefolia*, which contained a very interesting parasite. Externally it suggested the appearance of a Synchytrium, because of the numerous minute red dots distributed beneath the surface on the petioles and veins of the leaf and on the stem, although there was no gall formation similar to that caused by species of the Synchytriaceae. A section of the host, however, showed clearly that it was very different from any of the members of this family. Maceration or teasing of the host tissue revealed the presence of a mycelium, and the crowded condition of the fruit bodies suggested the genus Cladochytrium. Further study proved, however, that it was a unique type, very different from members of this genus. Since the material received was dead, it was impossible to obtain the zoospores, and Dr. STEVENS kindly promised to have fresh material sent me at stated times during the summer.

Beginning in the month of June, material was collected by Mr. J. G. HALL, assistant in botany at the North Carolina Agricultural College, and mailed once a week. Entire plants were collected, the roots were washed, and then packed mostly in pasteboard boxes with wet sphagnum. In this way they reached me in two or three days after shipment in very good condition, so that some of the parasitized ragweed plants were transplanted in the open and others in pots where they continued to grow.

From a study of this material I have been able to obtain the zoospores from the temporary zoosporangia and to work out certain stages in the life-history of the parasite. While searching the literature for unique forms of plant parasites, I discovered that this plant had been described fifteen years ago.

This remarkable parasite is *Rhodochytrium spilanthidis* Lagerheim.[1] It was first discovered by LAGERHEIM in 1889 near Quito, Ecuador, and later was observed by him in other provinces of Ecuador. In Ecuador it is parasitic on the stems and leaves of a species of Spilanthes, one of the

[1] LAGERHEIM, G. DE, Rhodochytrium, nov. gen., eine Uebergangsform von den Protococcaceen zu den Chytridiaceen. Bot. Zeit. 51:43–53. *pl. 2.* 1893.

Compositae. LAGERHEIM searched diligently but in vain to find it on other genera of plants. Its discovery in North Carolina, therefore, is a matter of considerable interest, not only because it naturally occurs on a different host, but because of its existence in the north temperate zone as well as the temperate section (mountain regions) of the tropics. Its North American host, *Ambrosia artemisiaefolia*, is not very distantly related to the South American host Spilanthes, the former belonging to the section Heliantheae-Ambrosiinae, while the latter belongs to the section Heliantheae-Verbesininae.[2] The question of its distribution becomes an interesting one, as to whether it is distributed over the intervening territory of Mexico, Central America, Panama, and other tropical countries; or whether it has been by chance imported from one country to the other through commerce; or finally whether ages ago, when the territory from the southern United States to Ecuador may have had a different climate, the parasite might have existed throughout this range, but now is separated by a tropical belt. I hope that collectors may be on the lookout for it in other parts of the United States and also in the intervening tropical region. I should be very glad to receive material in order to obtain further information as to its distribution.

The form of the plant may be briefly described as follows: When mature it may be likened to a miniature flask with a long slender tortuous neck; while from the base, or from the sides or both, rhizoid-like processes extend, which branch profusely in a very peculiar and characteristic manner. In general its form might be likened to that of a giant Entophlyctis, one of the chytridiaceous endobiotic parasites of the algae. In its development the zoospore, at rest on the epidermis, germinates, the germ tube enters between the cells and moves on toward a fibrovascular bundle where it branches, the branches making their way between the cells parallel with the bundles, so that on the stem the mycelium extends both upward and downward. On the leaves the parasite is also confined to the vascular bundles. The entire mycelium at certain stages of development is crowded with a reddish-yellow oil, which at maturity of the temporary zoosporangia, or of the resting sporangia, is withdrawn along with the protoplasm into the main body of the plant. The zoosporangium rests within or on a fibrovascular bundle and arises by a swelling of the mycelium at the point where the entering germ tube branches. The sporangia vary greatly in shape. They are oval, subtriangular, elliptical, etc., and vary from 50 μ in diameter (the smaller ones on the leaf) to 200–300 μ. The terminal mycelium is provided with numerous short haustoria, many of which are applied very closely to the spiral ducts. In the resting sporangia the wall

[2] See HOFFMAN in ENGLER AND PRANTL, Pflanzenfamilien 4[5]: 220 and 226.

of the mycelium next to the fruit bodies becomes very thick, also that of the entering germ-tube, while the wall of the zoospore in all of the plants remains as a small trumpet-shaped expansion of the end of the tube on the surface of the host. Starch grains are abundant in the larger portions of the mycelium and in the sporangia. The wall of the resting sporangium consists of three layers, the inner being laid down by the protoplasm after its accumulation in the main part of the plant body, and is thus not continuous with the mycelium which, however, usually becomes plugged after the withdrawal of the protoplasm. The walls of the resting sporangia are yellow at maturity, while the content is dark red.

The temporary zoosporangia have a thinner wall than that of the resting sporangia, and at maturity develop a stout exit tube, the end of which opens by a pore, the margin of which grows inward by invagination. The zoospores when swimming rapidly are elliptical in form, with the red oil in minute drops at the forward end, where are the two cilia. As they slow down they become rounded and are 8–10 μ in diameter.

LAGERHEIM considered this plant to be an alga devoid of chlorophyll, though LINDAU[3] says that on account of the lack of chlorophyll it cannot be classed with the algae.

The alga to which Rhodochytrium appears most closely related, according to LAGERHEIM, is Phyllobium, discovered by KLEBS[4] (*Phyllobium dimorphum* in leaves of *Lysimachia nummularia* and more rarely in *Ajuga reptans*, *Chlora serotina*, and *Erythraea centaurium; Phyllobium incertum* in dead Carex leaves). It is an intercellular parasite and *P. dimorphum* has also a definite relation to the vascular bundles. In this species the enlarged portion of the plant body contains chlorophyll in the protoplasm, as well as a reddish-yellow oil and starch. The branched rhizoid processes are devoid of chlorophyll. Resting spores only are known. They are packed with the reddish-yellow or orange-red oil and starch and possess a thick wall with several layers. The zoospores are biciliate.

A more extended paper is in preparation, dealing fully with the question of development, morphology, physiology, and cytology of this remarkable plant. This note is published in the hope that it will stimulate a search upon the ragweed and other possible hosts for this parasite, and I should consider it a great favor to receive material from different observers in case it is found.—GEO. F. ATKINSON, *Cornell University.*

[3] ENGLER AND PRANTL, Pflanzenfamilien 1[1**]:528. 1900.

[4] KLEBS, G., Beiträge zur Kenntniss niederer Algen formen. Bot. Zeit. **39**:249–257, 265–272, 281–290, 297–308, 313–319, 329–336. *pls. 3, 4.* 1881.

NOTE ON BALANCED SOLUTIONS

Some statements by Professor W. J. V. OSTERHOUT in the February number (p. 125) of the BOTANICAL GAZETTE in reference to balanced solutions require correction.

1. Balanced solutions, which are *not* complete culture solutions, were constructed and described[1] by me in 1892.

2. A balanced solution, which is at the same time a complete culture solution, is the solution of KNOP, proposed about sixty years ago. The "confusion" supposed by OSTERHOUT does not exist in this particular.

3. OSTERHOUT claims to have discovered an antagonistic action of potassium to magnesium. But I observed long ago that secondary potassium phosphate can retard the poisonous action of magnesium sulfate;[1] and also that another potassium salt—the monopotassium phosphate—*accelerates* the poisonous action of magnesium sulfate.

4. OSTERHOUT claims to have discovered a poisonous action of potassium salts. But I have observed Spirogyra alive for three weeks in a 0.3 per cent. solution of KCl[2], and alive for ten weeks in a 0.1 per cent. solution. In a 0.3 per cent. solution of K_2SO_4, the alga cells remained alive for over four weeks. The definition of OSTERHOUT, therefore, must be restricted to certain conditions. I have deprived young barley plants of endosperm, and kept them alive in 300^{cc} of a 0.5 per cent. solution of K_2SO_4 for over two months. Is it possible that here the small amount of magnesia in the plants has counteracted the "poisonous" action of the large amount of potassium salt?

5. A pupil of OSTERHOUT claimed recently to have discovered a poisonous action of calcium salts. This is not in accordance with my observation that Spirogyra can remain alive for over sixty days in a 1 per cent. solution of KCl. "Poisonous," however, is a relative and elastic term. The favorable effect of lime upon the development of root hairs, mentioned by that author, I observed long ago.[3]

6. I cannot agree with the opinion that the antagonistic relation of potassium to magnesium has the same cause as that of calcium to magnesium. I suggested an explanation of the poisonous action of magnesium sulfate, and also of the antagonistic action of calcium salts, in 1892.[4]

[1] Flora **75**:382. 1892.

[2] LOEW, O., AND ASO, K., On physiologically balanced solutions. Bull. Coll. Agric. Tokyo **7**:no. 3. 1907.

[3] Flora **75**:384. 1892; Bull. Bureau Pl. Industry, no. 45, pp. 51, 52.

[4] Flora **75**:376, 383. 1892; Bull. Bureau Pl. Industry, no. 45. My explanation has been adopted by one author, from somewhat similar observations, but without giving credit.

Since my views hold good also for the animal body, it gave me great satisfaction when MELTZER and AUER[5] published recently a series of wonderful experiments on the living animal, from which they inferred that "the continuation of the studies led up finally to the discovery that *calcium is rather the strongest antagonist to the inhibitory effects of magnesium.*" This is exactly what I have claimed for plants!—OSCAR LOEW, *Munich, Germany.*

FORMATION OF ADVENTITIOUS ROOTS IN THE UMBRELLA CHINA TREE

(WITH TWO FIGURES)

A curious case of "self-eating" may occasionally be found in hollow and decaying trunks of the umbrella China tree (*Melia Azedarach umbraculifera*). During a heavy storm in July, 1908, several large trees of this kind were blown down, the breaks occurring at the point where the main

FIG. 1 FIG. 2

[5] Amer. Jour. Physiol. **21**:403. May 1908. Communication from the Rockefeller Institute, New York. These brilliant investigations obscure all others made with such salts on animals.

trunk had been sawed off many years previously. Adventitious sprouts had grown out at the top and around the edges of the stump, and had formed a complete circle of stout limbs. In time these limbs will completely heal over the cut surface so as almost to obliterate the wound. The wood of the stump soon decays, however, and into this decaying mass there project dense mats of adventitious roots which spring from the point of origin of the limbs. These roots descend through the decaying materials and often, upon reaching the harder, less decayed wood of the lower part of the stump, turn sharply back and grow upward even to the point of origin. Fine fibrous roots may be found working down into the harder portions. *Fig. 1* shows a portion of a tree which had broken off about six feet from the ground; the roots shown are about two feet long. *Fig. 2* shows a limb that had broken off from a stump. The bent roots in the center were originally so sharply bent as to bring the parts parallel, but were separated for photographing. It will also be seen from this photograph that adventitious roots may arise from any part of the inner wall of the decaying stump.—O. M. BALL, *College Station, Texas.*

CURRENT LITERATURE

BOOK REVIEWS

The Bonn Textbook

A new English edition[1] of this well-known textbook may be made the occasion to refer to the contrast between German and American instruction in botany. It is perhaps safe to say that the *Bonn textbook* is the most extensively used text in Germany, and that in its English translation it dominates in American colleges. And yet, from the American standpoint it is more a book of reference than a textbook in the usual sense. Its organization and its demands are peculiar to the German mind and the German system of education. To divide a book into "general botany" and "special botany," and especially to discover that these titles are arbitrary rather than significant, suggest some rigid, old-fashioned curriculum rather than a logical presentation. "General botany" that includes no contact with the great groups, no basis for the evolution of the plant kingdom, no large conception of any kind, is surely a misnomer. It is made to include "morphology," a morphology that does not consider the development of groups, which means a long-abandoned morphology. Then this morphology (170 pp.) is divided into "external morphology" and "internal morphology" (subtitle "histology and morphology"). The "external morphology" is really the old type, when "flowering plants" furnished almost the only material of botany. It is not a question as to the accuracy of the facts, or to their importance, but simply a question of organization. Such an organization does not represent the development of botanical science today, and it does harm if it leads the student to a misconception of the content of the great divisions of botany. Nor is the organization and presentation of this so-called "morphology" its only antique flavor; for when one finds in the textbook sections on the "metamorphosis" of shoots, of leaves, of roots, he wonders why this point of view has never been changed.

The section on physiology (153 pp.) by the late Dr. NOLL is in the main an excellent and well-ordered presentation of the facts, though here and there it has not been revised to date. Thus, the fable of the ant plants still appears with all its frills (p. 235), and the physics of absorption is decidedly antique. The peculiarity of this section most open to criticism is the remarkably vitalistic attitude of the author. To say that "any attempt to explain vital phenomena solely by chemical and physical laws could only be induced by a false conception

[1] STRASBURGER, E., NOLL, F., SCHENCK, H., KARSTEN, G., A text-book of botany. Third English edition, revised with the eighth German edition, by W. H. LANG. pp. x+746. *figs.* 779. London: Macmillan & Co. 1908.

of their real significance and must lead to fruitless results," is to decry all investigation; for that is just what every physiologist in the twentieth century is doing. That "physical attributes . . . . can never explain qualities like nutrition" is a bold prophecy and a most discouraging one, though we be yet far from that goal. "Strictly physical and chemical processes" are contrasted with "strictly vital" ones, in that with the latter it "becomes impossible to predict what effect a particular cause will produce." True; but only because we do not know enough. NOLL disclaims "vital force" in terms, but constantly writes as though it were a necessary assumption.

The second part, entitled "Special botany," is doubtless the part of the book that gives it its deserved rank among texts. It is really and dominantly modern morphology as to facts, but not in spirit. It is a well-selected thesaurus of morphological information, in using which one feels a certain measure of confidence, and this is what has made the book indispensable. But the controlling spirit of morphology is lacking, because there is no conception of continuity in the plant kingdom. To an American teacher of botany this means that the facts are dumped down in piles, with no attempt to use them in the organization of a structure. It is good science, but poor teaching; and that seems to be the general method of instruction in German universities. This is not intended as a criticism, but merely as the statement of a distinction.

"Special botany" comprises "Crytogams" and "Phanerogamia." Note the incongruous forms of the two names, and the perpetuation of the old notion that a great chasm is fixed between cryptogams and seed-plants. Through the cryptogams and gymnosperms and the introductory part of angiosperms one breathes, for the most part, the atmosphere of modern morphology; but after that there are 170 pages dealing with the details of the classification of "Monocotylae" and "Dicotylae." And here comes a demand on the German student that fills the American teacher with amazement. It simply means that students in medicine and pharmacy are driven into these courses in botany; that it is supposed to be good for them to digest this encyclopedic information about groups of plants; that the German professor of botany cannot dispense with the fees of these students; and that all German textbooks on botany must contain this dreary waste of pages. We would suggest that this German educational necessity should not appear in the English translations, for it needlessly enlarges the book for American use.—J. M. C. and C. R. B.

Plant anatomy

Under this title STEVENS has written a book[2] which deals with the development and functions of plant tissues. Structure and function are so intermixed, and rightly, that there is no anatomical part of the book as distinct from the

[2] STEVENS, WILLIAM CHASE, Plant anatomy, from the standpoint of the development and functions of the tissues, and handbook of micro-technic. pp. xii+348. *figs. 136*. Philadelphia: P. Blakiston's Son & Co. 1907. $2.

physiological. In a review, however, the description of structures and of their functions may be mentioned separately.

In the days of the SACH'S régime, introduced into this country by BESSEY, the detailed study of tissues was a prominent feature of botanical instruction. It was gradually eliminated because of the growing demand for details that were thought to be significant in the evolutionary history of plants. A fact without a suggestive and large meaning came to be regarded as not worth while in elementary teaching. Doubtless this elimination of the study of tissues as such went too far, and a generation of botanists has been developed with too little knowledge of this kind. Then came the wonderful modern revival of anatomy so far as the vascular system is concerned, but this revival had to do with the evolution of vascular plants. STEVENS has carried us back again into the old atmosphere of tissues, but he has sought to avoid the old deadness of the subject by relating tissues to their functions. The spirit that animates the "skeleton," therefore, is physiological and ecological, and not the conception of evolution. The tissues are well described and illustrated, for STEVENS is an excellent teacher; and the text and drawings have been prepared in large measure directly from material under observation. It is to be regretted, however, that no trace of the modern vascular anatomy appears. For example, the remarkable development of knowledge in reference to the relation between the vascular anatomy of monocotyledons and dicotyledons would seem to have deserved mention. It may be claimed that relationship is not being considered, but this particular relationship has to do with previous misconceptions as to the actual structure of the vascular anatomy of monocotyledons.

Remembering that this is a book on physiological anatomy and not a textbook of plant physiology, we may properly commend the presentation of such topics as come within its scope. That is far less comprehensive than the well-known work of HABERLANDT, and the matter is far more elementary. The topics presented are chiefly those of entry and exit of materials, their movement in the plant body, and the processes of nutrition in the broadest sense. These are presented simply, clearly, and in the main accurately. Clever diagrams have been freely used, and they fulfil well the author's design of rendering more real the processes described. If they have any fault it is perhaps in tending to make conceptions too formal. Growth movement and the extensive phenomena of irritability do not come within the author's plan.

One unfortunate conception, embodied in chapter headings, and wrought into the text, is that of "circulation" of water and foods in "circulatory tissues." This idea dies hard, and we are sorry it has a new lease of life in this book.

The final chapters deal with the preparation of sections, use of the microscope, reagents and processes, the michrochemistry of plant products (not always reliable), and the detection of adulterations (too short to be really useful).—J. M. C. and C. R. B.

Bokorny's Textbook

BOKORNY has published a textbook of botany[3] that meets the official requirements for instruction in the *Oberrealschulen* and *Realschulen* of Bavaria. It appears in two parts and is thoroughly well printed and illustrated. The authorship of the book is a guarantee of its accuracy, and therefore the chief interest lies in discovering the kind of botanical material that is thought appropriate for the German student who is approximately the equivalent of our students from the third year of high school through the second year of college. In short, the purpose of the book would be about the same as that of most of our texts for high schools, which are announced for high schools, but are really suitable for colleges.

It is evident at first glance that the demand is for a general survey of the whole domain of botany. The first section (145 pp.) deals with "flowering plants," and is introduced by studies of common garden forms, the first contact being with rape and the various cabbage types. In this way a knowledge of the gross morphology of angiosperms is developed; to which is appended what would seem to be a few useless pages of cryptogams. The second section (15 pp.) deals with "inner morphology," which is explained to be "plant anatomy" or "histology." Yeast, pine needles, starch grains, chloroplasts, growing points, vascular elements, root-hairs, etc., form the usual débris under such a caption. The third section (197 pp.) is a presentation of the classification of the plant kingdom, that amazing impossibility that rides every German text like the old man of the sea. It is like inserting a dictionary of the language into the midst of a course on literature. We presume that the German boy must submit to it, but we wonder at his docility. This closes the first volume.

The second volume includes four sections. The first (20 pp.) is really a presentation of plant symmetry, but it is not long enough to hurt; the second (104 pp.) deals with physiology and anatomy, relating structure to function; the third (90 pp.) is entitled "biology," which we include under the broader term ecology, and it looks quite modern and interesting; the fourth (17 pp.) is a brief outline of plant geography, being chiefly an enumeration of zones, provinces, etc.

The general structure of the book would not be so very different from that of the corresponding American texts, were the 200 pages of classification omitted. —J. M. C.

MINOR NOTICES

Bibliographia Linnaeana.—This work[4] represents the most complete bibliography of the numerous Linnaean publications ever compiled. The different works of LINNAEUS and the publications of other authors directly relating thereto are arranged chronologically, beginning with the *Dissertatio botanica de planta*

[3] BOKORNY, TH., Lehrbuch der Botanik für Oberrealschulen und Realschulen. Teil I, pp. vi+366, *M*4. Teil II, pp. 233, *M*3. Leipzig: Wilhelm Engelmann. 1908.

[4] HULTH, J. M., Bibliographia Linnaeana: Matériaux pour servir a une bibliographie Linnéenne. Partie 1, Livrasion 1, 8vo. pp. 170. *pls. 1–3, 5–9, 11.* Uppsala: Librairie de l'Université, C. J. Lundström. Berlin: R. Friedländer & Sohn. 1907.

*Sceptrum Carolinum dicta, quam * * * praeside Laurentio Robergio * * * ventilandam sistit auctor Johannes Olavus Rudbeck Ol. Fil. * * * 1731.* After mentioning the original edition of the respective works, subsequent editions, reissues, and translations are accurately recorded; and in each instance the usual information is given as to place and time of publication, as well as the form, number of pages of text and index, and other details. In those works consisting of more than one volume the subjects treated in each volume and the number of pages devoted to each subject are indicated briefly in tabulated form. Reference is also made to contemporary notices and reviews.

The volume is amply provided with cross-references, and the subject-matter on the pages is well differentiated by judicious spacing and a careful selection of type, thus making the work attractive in appearance and of easy reference. Several facsimile reproductions of title-pages and frontispieces of the rarer Linnaean works are appended, which add to the interest of the volume. It is a book which will serve as a most useful guide to the Linnaean literature.—J. M. GREENMAN.

The flora of Styria.—VON HAYEK[5] has begun a systematic treatment of the ferns and flowering plants of Styria. The first number of this work contains a key to the main groups and sub-groups, which are clearly defined, and a second key leading directly to the families. The enumeration of species follows a natural sequence, beginning with *Ophioglossum vulgatum* L. and continuing through the three parts to *Chenopodium album* L. A concise description of each species is given in German, and associated with it one finds a fairly complete synonomy and bibliography. Careful attention has been given to habitat and distribution. Text figures are introduced to illustrate certain groups, but the illustrations lack clearness and detail. The nomenclature is in accordance with the Vienna Rules adopted at the last International Botanical Congress.

On the whole the work thus far happily combines a semipopular presentation and a degree of scientific accuracy which will make it useful to the local botanist and to the general systematist.—J. M. GREENMAN.

Flowering plants and ferns.—Under this title WILLIS published the first edition of his manual and dictionary in 1897. A second edition appeared in 1904, and now a third[6] has come to hand. The purpose of the book is "to supply, within a reasonable compass, a summary of useful and scientific information about the plants met with in a botanical garden or museum, or in the field." The result is a very convenient book of reference. The first part presents an

[5] VON HAYEK, AUGUST, Flora von Steiermark. Eine systematische Bearbeitung der im Herzogtum Steiermark wildwachsenden oder im Grossen gebauten Farn- und Blütenpflanzen nebst einer pflanzengeographischen Schilderung des Landes. Vol. I. Parts 1–3. 8vo. pp. 240. Berlin: Gebrüder Borntraeger. 1908

[6] WILLIS, J. C., A manual and dictionary of the flowering plants and ferns. Third edition. pp. xii+712. Cambridge: The University Press. 1908. New York: G. P. Putnam's Sons. $2.75.

outline of the morphology, natural history, classification, geographical distribution, and economic uses of the flowering plants and ferns. The second part, to a great extent rewritten, is a dictionary of the classes, cohorts, families, and chief genera, alphabetically arranged. The third part, to which much has been added, is a glossarial index of English names, economic products, technical terms, specific names, etc. Altogether the volume is a most convenient one for any botanist or botanical laboratory.—J. M. C.

Library of John Donnell Smith.—In 1905 JOHN DONNELL SMITH presented to the Smithsonian Institution his herbarium, containing over 100,000 mounted specimens, and his botanical library, containing about 1600 bound volumes. The herbarium has been placed in the U. S. National Museum; but for the present the library is to remain in Baltimore. The collection of books is chiefly taxonomic, and is especially rich in the literature of the floras of Mexico and Central America. This valuable collection has been placed freely at the disposal of botanists, and a very complete and handsome author catalogue has been issued by the Smithsonian Institution as a special publication,[7] in addition to the regular edition (Contrib. Nat. Herb. Vol. XII. part 1). This disposition of his exceedingly valuable herbarium and library emphasizes not only the generosity but also the scientific spirit of the donor.—J. M. C.

Cryptogamic flora of Brandenburg.[8]—The third part of the volume on Algae by LEMMERMANN has just appeared. It is devoted entirely to the Flagellatae, all of the recognized seven "orders" excepting the last (Euglenineae) being presented, and that one is begun.—J. M. C.

NOTES FOR STUDENTS

Paleobotanical notes.—NATHORST has begun the publication of an important series of paleobotanical memoirs.[9] The first deals with Pseudocycas, a new genus from the Cenomanian Cretaceous of Greenland. It has generally been considered that leaves of the Cycadeae made their appearance first in the Triassic, and thus considerably antedated the true Zamieae, which are known earliest from the Tertiary deposits. The author shows that leaves from Cretaceous deposits, which have been described by various authors as belonging to Cycadites or even to the living Cycas, are in reality not to be included in these genera at all, since they differ from the existing Cycas in that each leaf pinnule has a *double* midrib and is attached to the rachis by a broad instead of an attenuated base. On account of these divergences, the author sets up a new genus, Pseudocycas.

[7] Catalogue of the botanical library of JOHN DONNELL SMITH, presented in 1905 to the Smithsonian Institution. Compiled by ALICE CARY ATWOOD. Special publication, Smithsonian Institution. pp. 94. July 1908.

[8] LEMMERMANN, E., Kryptogamenflora der Mark Brandenburg. Band 3, Heft 3, Algen, 305–496. Leipzig: Gebrüder Borntraeger. 1908.

[9] Kung. Svenska Vetensk. Akad. Handl. **42**:no. 5. 1907; **43**:no. 3. 1908; **43**: no. 6. 1908.

The discovery of the duplicate character of the midrib is due to the microscopic examination of leaf pinnules. Four species are described under the new genus.

The second memoir is on the cuticle of *Dictyozamites Johnstrupi* Nath. By the microscopic study of the cuticle of this species, bleached with *eau de Javelle* and mounted in glycerin jelly, the author shows its close affinity with Otozamites as described by SCHENK.

The third memoir is devoted to the study of a lycopodineous cone from the Rhaetic of Schonen, which the author earlier described, with some reserve, as being of cycadaceous affinities, under the name *Androstrobus Scotti*. A microscopic examination of the cone in question, with the aid of *eau de Javelle* and other bleaching reagents, revealed the fact that it was of lycopodineous affinities, and the name is accordingly changed to *Lycostrobus Scotti*. The cone is attached to an apparently herbaceous peduncle about 2^{cm} in diameter and is about 12^{cm} in length. The minute structure of megasporangia and megasporophylls could not be made out. The megaspores were over 0.5^{mm} in diameter and were characterized by appendages along the triradiate ridges. The rest of the surface was covered with minute spines. The microspores, occurring in distinct clusters, were found in the upper part of the cone, were bifacial as in Isoetes, and were 30 to 50 μ in diameter. The author comes to the conclusion that Lycostrobus is more nearly allied to Isoetes than any living lycopod. This cone is of great interest from two standpoints. It illustrates how extremely unsafe conclusions as to affinities based on mere superficial characters must be, since *as an impression* the fossil was considered as belonging to the Cycadophyta. Also it goes a long way toward demonstrating that Isoetes is a true lycopod, and not an appendage of the fern series, as has been suggested by VINES, FARMER, and CAMPBELL.

The fourth memoir deals with the microscopic investigation of cuticles of fossil leaves, sporangia, spores, etc. Perhaps the most interesting result under this head is the demonstration that ARBER'S *Carpolithus Nathorsti* (1908) is in reality not a seed of a pteridosperm at all, as is supposed by that author, since the supposed seminal organs were shown by maceration to be microsporangia. Numerous abietineous winged pollen grains were found in material from the Trias of Hör. The author comes to the general conclusion: "die Gattung Pinus schon gegen das Ende der Triasperiode, in den nördlicheren Teilen der Erde ausgebildet war." This result appears not to be without significance in connection with present discussions in regard to the antiquity of Pinus. Smaller winged microspores were also found, which the author does not attempt to refer to any existing coniferous genus. It appears not improbable that they represent the microspores of certain of the Brachyphylloideae, a new subtribe of araucarian conifers described by Dr. HOLLICK and the reviewer.

In the fifth memoir the author throws additional light on *Nathorstia* Heer, first described as Daneites from the older Cretaceous of Greenland. By means of maceration he has been able to show that the fossil in question is allied to

the living marattiaceous genus Kaulfussia, but differs from it in having the ringlike sorus of sporangia multiseriate instead of simple.

In the sixth memoir *Antholithus Zeilleri* Nath. is discussed, which has been regarded as the staminate inflorescence of Baiera. It is shown that the fossils in question consist of dichotomously divided, dorsiventral organs, the ultimate divisions of which bore eight sporangia. Consequently they do not resemble the staminate flowers of the living Ginkgo.

Throughout the author gives paramount importance to the microscopic examination of his material, and suggests many ingenious and some novel devices for the preparation of the objects for the microscope.—E. C. JEFFREY.

Anatomy of Veronica and Gratiola.—The internal structure of the stem and leaf of about 60 species of Veronica and of *Gratiola officinalis* has been studied by HUCHEDÉ,[10] and his results constitute a very important and interesting contribution to the knowledge of the structure of these genera, especially of the former. The material examined consisted of species from Europe, Asia, Australia, and New Zealand, thus comprising both herbaceous and suffrutescent forms. So far as concerns the leaf and stem, the author has demonstrated that a considerable variation in structure exists in Veronica, in regard to epidermis, chlorenchyma, hairs, endodermis, and pith, and the petiole also offers several good characters for distinguishing a number of species. The species from New Zealand differ in a marked way from the European; for instance in regard to the chlorenchyma, which is mostly composed of palisades, unless it is bifacial; furthermore, by the veins (circular in cross-section) being imbedded in the chlorenchyma and supported by stereome or collenchyma. The stem of the New Zealand species contains but little pericyclic stereome, while the pith is frequently sclerotic. It is quite interesting to see that the author has observed some anatomical characters sufficient for distinguishing *V. virginica* L. from *V. sibirica* L., and *V. saxatilis* Scop. from *V. fruticulosa* L., which by many authors have been regarded as synonyms. Very few species are considered of any importance as medicinal plants, and our *V. virginica* (NUTTALL'S *Leptandra virginica*) is actually the only one which is recognized as such and is still in use (the rhizome).

The paper contains well-written anatomical diagnoses of these species, accompanied by a number of very fine drawings, showing their anatomical characteristics. It is only to be regretted that the root has not been considered, for there is no doubt that the structure of this organ must show variations of no small importance, when we bear in mind that among these species of Veronica are both terrestrial and aquatic types, annual and perennial, herbaceous and suffrutescent. The fact that the primary root persists in some of them, and that it becomes replaced by secondary roots in others, might also deserve notice.

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[10] HUCHEDÉ, J., Veroniques et Gratiole. Etude histologique et pharmacologique. Travaux Lab. Mat. Medic. Ecole Sup. Pharm. Paris **5**:137. 1907.

However, we admit that it is often very difficult to obtain material so well represented as to include the root-system, especially of herbarium specimens.—THEO. HOLM.

Anatomy of the leaves of Ranunculaceae.—GOFFART[11] has described the leaf structure of species representing 23 genera of Ranunculaceae, nearly all from the old world. The paper is illustrated by about 400 excellent figures of the leaf outline and the internal structure. So many anatomical details are recorded that an abstract in brief space is impossible.

The author has followed the method suggested by his teacher, the distinguished anatomist A. GRAVIS, to examine the leaf at very many places and at various stages of its development, and to give due consideration to the course of the mestome strands from stem to petiole and throughout the blade. In this way one obtains a most complete idea of the structural peculiarities, and such are highly welcome to students of affinities, expressed not only by floral structures but also by internal organization. Much has been written about the validity of several of these genera, considered from a systematic point of view, especially judging from the floral characters. It is therefore interesting to learn from this paper that, so far as concerns the leaf structure, Hepatica is not distinct from Anemone, and the same seems to be the case with Nigella-Garidella, Actaea-Cimicifuga, and Ficaria-Oxygraphis-Ranunculus. However, in respect to Oxygraphis, the author has examined only *O. Cymbalaria*, which in the reviewer's opinion is no true Oxygraphis, but a Ranunculus. An examination of *O. glacialis*, for instance, would no doubt have led to a different conclusion. On the other hand, Pulsatilla appears to be generically distinct from Anemone, and Batrachium from Ranunculus. Future investigations, for instance, of the singular North American representatives of Ranuculus constituting the section Crymodes, Cyrtorhyncha, and Pseudaphanostemma might lead to the segregation of these from Ranunculus altogether. For such a purpose GOFFERT'S contribution is a very important one; and it might be stated at the same time that the same family has been treated by other pupils of GRAVIS in regard to the structure of the pericarp and spermoderm, the embryo and seedlings, etc., the result of which have appeared in the *Archives* since 1897.—THEO. HOLM.

Prothallia of Kaulfussia and Gleichenia.—One of the results of CAMPBELL'S recent visit to Java is the publication of an account[12] of the prothallia of the oriental and monotypic Kaulfussia and of Gleichenia. The account fills in an important gap in our knowledge of the prothallia and sex organs of Filicineae; and it is of interest to note that the account satisfies the desire for completeness rather than the desire for new things.

[11] GOFFART, JULES, Recherche sur l'anatomie des feuilles dans les Renonculacées. Arch. Inst. Bot. Univ. Liège III. pp. 187. *pls. 14.* 1901. The editors feel justified in calling attention to so old a publication in view of the fact that it has an important bearing upon the current taxonomic study of the family.

[12] CAMPBELL, D. H., The prothallium of Kaulfussia and Gleichenia. Ann. Jard. Bot. Buitenzorg II. 7:69–102. *pls. 7–14.* 1908.

The prothallium of Kaulfussia is said to be the largest among Marattiaceae, a very large one reaching 2.5×1.75^{cm}; but the usual adult size is 1^{cm} or more in length and nearly as broad. An endophytic fungus is always present. The antheridia and archegonia, restricted to the ventral surface, are also of ususual size. CAMPBELL thinks that probably all the organs of the embryo of Marattiaceae, except the foot, are of epibasal origin, and he finds confirmation of this in Kaulfussia. As in other members of the family, the shoot pierces through the prothallium and emerges from the dorsal surface.

The prothallia of Gleichenia are also of the "massive-midrib" type, more or less lobed, and with an endophytic fungus. The antheridia are restricted to the ventral surface in all species except *G. laevigata*, in which they occur upon both surfaces. In the species examined they are larger and more complex than recorded in the species examined by RAUWENHOFF, the wall cells being much more numerous, several hundred sperm mother cells sometimes being produced, and an opercular cell probably always being present. The archegonia are more numerous upon the flanks of the "midrib" than upon its middle region; the necks are very long; and the neck canal cell (except in *G. polypodioides*) usually divides into two cells. The embryo, so far as the material permitted comparison, resembles that of the Polypodiaceae. The characteristic protostelic condition was observed in sporelings, but it was not discovered whether it persists in the adult form in all species.—J. M. C.

Sexual reproduction in the rusts.—During the last three or four years BLACKMAN and CHRISTMAN have described a process of sexual reproduction in the rusts. Their accounts are not in entire agreement, and so the ground has been traversed by OLIVE,[13] with an unusual wealth of material. About forty species were examined, and the most favorable form for the study undertaken proved to be *Triphragmium ulmariae* (Schum.) Link, on *Ulmaria rubra* Hill, a caeoma form similar to the species of Phragmidium studied by BLACKMAN and CHRISTMAN. The two fusing cells ("gametes"), as well as their nuclei, were found to be approximately equal, but for reasons given in detail it is concluded that they differ somewhat in time of development. The equality and sexual character of both the fusing cells are statements opposed to those of BLACKMAN. It is also concluded that the sterile cell (at the tip) is not an abortive trichogyne, but merely a "buffer cell" of the gametophyte. Conjugation takes place through a perforation developed in the contact-walls. It may begin through a very small conjugation pore (observed by BLACKMAN), but this is regarded as only the beginning of a larger perforation. In the study of the various vegetative nuclear divisions it was discovered that they are all mitotic, each nucleus during the conjugate divisions acting independently. These nuclear divisions, conducted with the aid of centrosomes, are described in detail; and in Triphragmium it was ascertained that the chromosomes are probably eight in number. The occur-

[13] OLIVE, EDGAR W., Sexual cell fusions and vegetative nuclear divisions in the rusts. Annals of Botany **22**:331–360. *pl. 22.* 1908.

rence of one or more multinucleate cells at the base of certain young aecidia is considered, and the conclusion is reached "that they are sporophytic structures, and that they result from the stimulated growth which follows the sexual cell fusions." This is opposed to the idea (CHRISTMAN) that the "fusion cell" functions at once as a "basal cell" at the bottom of each row of spores.—J. M. C.

Gnetales and Angiosperms.—Last year ARBER and PARKIN announced[14] their "strobilus theory of angiospermous descent;" and now they have applied it to the interpretation of the relationships of Gnetales.[15] There is much to commend their general view, without conceding all the details cited; in fact the reviewer has long since reached the same conclusions as to the character of the strobilus of Gnetales, and has remarked upon its similarity to such inflorescences as those of the Amentiferae. The authors do not regard the Gnetales as a modern group, although at present unknown as fossils. The three survivors of this ancient group have "pro-anthostrobili,"[16] evident in the staminate "flower" of Tumboa and reduced in the other "flowers" of the group by the suppression of one set of sporangia. To the authors the strobilus of this group is the so-called "flower;" and the strobilus of current terminology is an aggregate of strobili. Based upon this strobilus situation, the authors regard Gnetales as a phylum of gymnosperms having a common ancestry with angiosperms in the hypothetical "hemiangiosperms," and in many respects following parallel lines of development.—J. M. C.

Origin of angiosperms.—LIGNIER[17] has discussed the recent paper by ARBER and PARKIN,[18] in which the origin of the angiosperm flower (of the Ranales type) is traced to the bisporangiate strobilus of Bennettitales. From this view LIGNIER dissents, as he regards the strobilus in question as representing an inflorescence rather than a flower. To him the intraseminal scales are not sterile carpels or sterile lobes of carpels, but bracts in whose axils the ovuliferous stalks appear. This strobilus, therefore, is a compound one, as are the ovulate strobili of many of the Coniferales and both strobili of the Gnetales. LIGNIER agrees to the idea that the Ranales type of flower is the most primitive, but he would derive it from

[14] Review in BOT. GAZETTE **44**:389. 1907.

[15] ARBER, E. A. NEWELL, AND PARKIN, JOHN, Studies in the evolution of the angiosperms. The relationship of the angiosperms to the Gnetales. Annals of Botany **22**:489–515. 1908.

[16] An "anthostrobilus" is an axis bearing microsporophylls and megasporophylls, with the latter above the former. A "pro-anthostrobilus" is the variety in which the pollen reaches the ovules (gymnosperm), the strobilus of Bennettitales being an example; while a "eu-anthostrobilus" is the variety in which the pollen is received by the megasporophyll (angiosperm).

[17] LIGNIER, O., Le fruit des Bennettitées et l'ascendance des Angiospermes. Bull. Soc. Bot. France IV. **8**:1–17. 1908.

[18] BOT. GAZETTE **44**:389. 1907.

the earlier cycadophyte stock. Accordingly he introduces before ARBER and PARKIN'S "pro-anthostrobilus" an evolutionary stage characterized by the grouping of filicinean microsporophylls and megasporophylls in monosporangiate strobili, and to this hypothetical stage he gives the name "pteridostrobilus." This stage was temporarily a common one for the general cycad and angiosperm phyla; and at this stage the cycads practically stopped, with reduction of sporophylls; while the angiosperm phylum proceeded to the establishment of the bisporangiate condition, the evolution of angiospermy, the transformation of the habit of the vegetative body, etc. According to LIGNIER, the Bennettitales represent a different phylum, which branched from the cycadophyte phylum after the angiosperms, but still at the pteridostrobilus stage.—J. M. C.

Nitrogen fixing bacteria.—In a short preliminary paper[19] BREDEMANN summarizes the conclusions deduced from his study of nitrogen fixing bacteria of the Clostridium type. Eleven cultures of the so-called "species" of various authors were compared with sixteen types isolated by himself. These types were from many sources, particularly soil from different parts of the world. A comparison of these forms cultivated under proper conditions for considerable periods has convinced him that all must be considered as a single species, the *Bacillus amylobacter* A. M. et Bredemann. Some characters, such as size of spores, motility, and development on culture media, are quite constant; others, as the ability to ferment nitrogen free solutions, are variable. Indeed, the variability of subcultures from a single stock may be made, by appropriate methods, to exceed the differences among the various so-called species and races. Most important, perhaps, are his conclusions relative to variation in nitrogen fixing power. Old cultures which had completely lost this capacity regained it when grown for a time in soil properly sterilized. This ability to fix nitrogen is closely correlated with that of fermenting nitrogen free solutions, and varies as greatly among various subcultures from a single stock as among those types that have been described as different species. Continued cultivation brings loss of power to fix nitrogen, but this power may be regained by appropriate culture methods. —R. E. BUCHANAN.

Variations of sexual organs of Saprolegnia.—KAUFFMAN[20] has obtained some extremely interesting results from some unusually guarded cultures of the Saprolegniaceae. He has found it possible to isolate species of Saprolegnia quickly by means of a single zoospore, and such pure cultures were used in his experiments. A great variety of solutions was used, but the best substances to

[19] BREDEMANN, G., Regeneration der Fähigkeit zur Assimilation von freien Stickstoff des *Bacillus amylobacter* A. M. et Bredemann und der zu dieser Spezies gehörenden bisher als Granulobacter, Clostridium usw, bezeichnete anaeroben Bakterien (Vorläufige Mitteilung). Ber. Deutsch. Bot. Gesell. **26a**:362–368. 1908.

[20] KAUFFMAN, C. H., A contribution to the physiology of the Saprolegniaceae, with special reference to the variations of the sexual organs. Annals of Botany **22**: 361–388. *pl. 23*. 1908.

effect the production of sexual organs were haemoglobin and leucin, as found also by KLEBS. The effect of nutrition upon the differentiation of reproductive and vegetative processes was amply confirmed; but not all species produce sexual organs under the same conditions, showing a physiological as well as a morphological distinction. *S. hypogyna*, in which true antheridia do not develop, was made to develop antheridia under proper nutrient conditions. The variations induced were so extensive as to include all the characters used for diagnostic purposes, and the author makes the suggestion that a species can be defined in terms of its behavior in an established standard culture. The conclusion is reached that there are a great many entirely distinct forms, physiologically so at least, which may be regarded as elementary species in the sense of DEVRIES. The whole tendency of the investigation is to confirm the doctrine that sex in plants is determined by external conditions.—J. M. C.

The sporangiophore.—Miss BENSON[21] has emphasized the morphological importance of the sporangiophore, and has extended its application. Originally applied in Sphenophyllales, Equisetales, and Psilotales, she would extend its application to all pteridophytes. Objection is made to BOWER'S application of the term in Ophioglossales to the "fertile spike." In the Filicales the sorus (or synangium) is the sporangiophore; while in Lycopodiales it appears in a "reduced" form as the subarchesporial pad. Primarily it is a unit structure that appears on the axis, but may be "taken up on to" the leaf, as in all known ferns and many Lycopsida. The definition suggested is that "a sporangiophore is a structure characteristic of the sporophyte of Pteridophyta, and consists of a central, generally pedicellate mass of sterile tissue, with sporogenous regions occupying one or more sporangia, which may be terminal, lateral, or basal." It is further suggested that even Cordaitales and Taxineae may be forms whose sporangiophores have never been "taken up" on leaves. All this means a monophyletic origin for pteridophytes, with the sporangiophore (as now defined) as a fundamental and unifying structure of the sporophyte. Such a hypothesis is worth thinking about, and it has enough facts to support it to make it seductive.—J. M. C.

Schizostely in Gramineae.—Schizostely has been seldom observed among the flowering plants, the recorded cases being in certain representatives of Alismaceae, Nymphaeaceae, Cabombaceae, and Ranunculaceae. Recently VAN TIEGHEM[22] has discovered this singular structure in *Sorghum halepense* Pers. So far only the monostelic structure has been observed in the aerial and subterranean stems of the numerous Gramineae examined. While the aerial stem of this Sorghum is monostelic, the rhizome possesses a large number of meristeles

[21] BENSON, M., The sporangiophore—a unit of structure in the Pteridophyta. New Phytol. 7:143–149. 1908.

[22] VAN TIEGHEM, PH., Une graminée à tige shizostélique. Ann. Sci. Nat. Bot. IX. 5:371. 1907.

in the cortex, which are of a very different size, but each is surrounded by a special and very plainly differentiated endodermis, in which the Casparyan spots are readily noticeable. The structure of the mestome strand in each is typical, and does not differ from that known so well from the Gramineae in general. The fact that the endodermis is differentiated at a very early stage, and that the inner cell walls become thickened long before the vessels and the adjoining tissues become lignified, makes this schizostelic structure plainly visible in the young rhizome, in the internodes, and partly also in the nodes. It would be interesting to know whether the structure is not to be found in other grasses.—THEO. HOLM.

Morphology of Podostemaceae.—WENT[23] has made some remarkable observations on the ovule of Podostemaceae. He has obtained abundant material and finds the several species studied very consistent with one another and very inconsistent with other Angiosperms. A future more extensive paper is promised, which will deal with all the features of the family.

The outer integument develops first and forms the micropyle. Later the inner integument develops, but never incloses the embryo sac region of the nucellus. The hypodermal megaspore mother cell caps an axial row of cells, which first elongate and then disorganize, resulting in a pseudo-embryo sac inclosed by the inner integument. The true embryo sac enlarges but little, and the embryo grows into and occupies the pseudo-sac. After the first division of the megaspore nucleus, the primary antipodal nucleus degenerates promptly, so that there are no antipodal cells and no antipodal polar nucleus. The four micropylar nuclei form as usual, but the micropylar polar degenerates promptly, so that there is no "double fertilization" and no endosperm. It is to be regretted that alcoholic material and scattered stages did not permit absolute certainty on many points.—J. M. C.

Tracheae of ferns.—GWYNNE-VAUGHAN[24] has investigated the xylem of some of the recent ferns, and concludes that the current statement that the metaxylem of Filicales consists for the most part of scalariform tracheids is "thoroughly misleading," and that "a return must be made to the views held by the earlier anatomists (DIPPEL, SACHS, WEISS), who believed that the xylem elements of the ferns in general were true vessels and not tracheids at all." The investigation was induced by studies of certain fossil Osmundaceae, in collaboration with KIDSTON. The conclusions are that the xylem elements of pteridophytes are mostly vessels with true perforations in their longitudinal as well as in their terminal walls. In the Osmundaceae, *Nephrodium Filix-mas*, and probably others, a special type of vessel occurs which is characterized by the complete disappearance of the primary tracheal wall at certain points, so that the cavities of the pits are vertically continuous in the middle of the wall. It is probable that

[23] WENT, F. A. F. C., The development of the ovule, embryo sac, and egg in Podostemaceae. Recueil Trav. Bot. Néerland. **5**:1–16. *pl. 1.* 1908.

[24] GWYNNE-VAUGHAN, D. T., On the real nature of the tracheae in the ferns. Annals of Botany **22**:517–523. *pl. 28.* 1908.

more or less rounded pits preceded the transversely elongated pits of the scalariform type in the Filicales.—J. M. C.

Origin of Sphenophyllales.—In 1903 LIGNIER[25] published his view that the Equisetales and Sphenophyllales are of filicinean origin. Recently this disposition of the Sphenophyllales has been opposed, especially by SCOTT, and by the anatomical work of Miss SYKES. LIGNIER has now resumed the discussion[26] and reaffirms his former position, with additional argument. He claims that the "fertile leaves" of Sphenophyllum cannot be homologized with the sporangiferous structures of Tmesipteris; but that their "sterile pinnules" are comparable with those Archaeopteris. The "fertile pinnules," at the same time, are of the same type as those of the Primofilices. Therefore, LIGNIER concludes that the Sphenophyllales ought to be "attached" to the Primofilices and not to the Lycopodiales. A number of secondary characters also are used to strengthen this view.—J. M. C.

Sieve tubes.—An elaborate histological investigation of the details of development in sieve tubes of angiosperms has been made by HILL.[27] It appears that the young cell wall which is to form a sieve plate, is at first pitted, the pit-floor being penetrated by one or a group of fine protoplasmic threads, which, after some change of the adjacent cell wall, "begin to be bored out to form slime strings, apparently by a ferment." These slime strings enlarge and merge, so that finally one large slime string occupies the place of the group. This is always inclosed in a protoplasmic tube, which lines each pore of the plate, and the pore itself has a callus lining covering the cellulose part of the wall. Many further details are given and the usual teleological causes assigned for the processes. The paper contains an excellent historical summary.—C. R. B.

Hygroscopic movements.—STEINBRINCK and SCHINZ, by studies on some desert plants, support further the view that the internal structure of the thickened walls, as well as differences in the tissues, are the cause of the warping movements of fruits and other parts.[28] They find that lignified walls really swell and shrink more than cellulose walls, and they attribute to differences in structure the unlike polarization phenomena observed in the walls of different layers of cells in the bending organ. Incidentally they establish the "true" Jericho rose as *Anastatica hierochuntica* L., and not *Odontospermum pygmaeum* (DC.) Benth. & Hook.—C. R. B.

[25] LIGNIER, O., Equisétales et Sphenophyllales. Leur origine filicinéene commune. Bull. Sci. Linn. Normandie V. **7**:93. 1903.

[26] LIGNIER, O., Sur l'origine des Sphénophyllées. Bull. Soc. Bot. France IV. **8**:278–288. 1908.

[27] HILL, A. W., The histology of the sieve tubes of angiosperms. Annals of Botany **22**:245–290. *pls. 17, 18. figs. 13.* 1908.

[28] STEINBRINCK, C., and SCHINZ, H., Ueber die anatomische Ursache der hygrochastischen Bewegungen der sog. Jerichorosen und einiger anderer Wüstenpflanzen. Flora **98**:471–500. 1908.

Biology of diatoms.—Cell division is described by BERGON[29] for Biddulphia, but the nuclear details are not shown. No centrosomes are figured. The principal point of interest in the formation of auxospores is that not one, but two are formed in each cell. Spores (the so-called microspores) have been described and the observations have been disputed. Although the existence of such spores might safely be conceded, this paper describes the development of sporangia and spores so clearly that there can be no doubt either as to their existence or the mode of their formation.—CHARLES J. CHAMBERLAIN.

Sterile anthers of Ribes.—JANCZEWSKI[30] has discovered an interesting situation in the pollen of Ribes. In the genus there is every stage between entirely fertile and absolutely sterile anthers. Certain subgenera and a few hybrids habitually develop perfect pollen. Most common among the hybrids, however, is a mixture of sterile and fertile pollen grains, in varying proportion. In certain hybrids and in the subgenus Parilla the pollen is persistently inert. Degeneration generally occurs after tetrad formation, but sometimes in the mother cell stage.—J. M. C.

Protoplasmic rotation.—BIERBERG[31] concludes that rotation and streaming is neither a widespread nor usually a normal phenomenon, but he does not accept Miss KELLER'S view that it is a symptom of dying. On the contrary, he finds that it accelerates the transfer of materials more than threefold over diffusion alone. His attempts to account teleologically for the existence of these movements in water plants, according as they have or have not conducting tissues, or are or are not permeable in all parts, are less valuable than his experimental work.—C. R. B.

Rusts.—OLIVE[32] has published a popular account of cereal rusts and their life-histories. He confesses that "the problem of the prevention of rusts is such a difficult one that many points still remain to be solved;" and states that "the main thing which can be done at present is simply to record the present status of our knowledge as to the nature of these complicated organisms, and to awaken interest in a knowledge of their habits."—F. L. STEVENS.

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[29] BERGON, P., Biologie des Diatomées.—Les processus de division, de rajeunissement de la cellule et de sporulation chez le *Biddulphia mobilensis* Bailey. Rev. Gén. Botanique IV. **7**:327–358. *pls. 5–8.* 1907.

[30] JANCZEWSKI, ED., Sur les anthères stériles des groseilliers. Bull. Acad. Sci. Cracovie **1908**: 587–596. *pl. 24.*

[31] BIERBERG, W., Die Bedeutung der Protoplasmarotation für den Hofftransport in den Pflanzen. Flora **99**:52–80. 1908.

[32] OLIVE, E. W., Rusts of cereals and other plants. S. Dak. Agric. Exp. Sta. Bull. 109. June 1908.